Phytoplankton dynamics in two large rivers: long-term trends, longitudinal dynamics and potential impacts of climate change

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1 General Introduction

Phytoplankton forms an important basis of aquatic food webs. These unicellular organisms are the most important primary producers in many surface waters. Also in large rivers, internal primary production derived from phytoplankton is a main source of organic matter for organisms on higher trophic levels (Thorp and Delong 1994). While plankton dynamics have been studied extensively in lentic fresh waters such as lakes and reservoirs, comparatively little research has focused on factors that regulate phytoplankton biomass in lotic waters (Basu and Pick 1995; Reynolds 2000). Plankton biomasses in rivers are regulated by hydrological (discharge, water residence time), physical (light, temperature), chemical (nutrient concentrations), and biotic factors (predation, competition) (Reynolds 1988; Moss et al. 1989). However, it is insufficiently known how these individual factors act in concert, and how phytoplankton responds to changes in these environmental conditions.

High reproduction rates which are typical for unicellular plankton organisms are beneficial in river ecosystems because they can reproduce fast when water retention times are short (Viroux 1997). In the downstream reaches, the density of river plankton is generally highest (Vannote et al. 1980), due to longer retention times. Especially in spring, strong phytoplankton growth rates can lead to phytoplankton mass developments, so called spring blooms, which can have a large impact on water quality and ecosystem function (Gallegos and Jordan 2002). It can be assumed that in spring, the biological variables strongly depend on the rapidly changing environmental factors. Thus, the analysis of long-term trends, including the appropriate detection of cardinal dates during spring blooms, is a useful tool to identify relevant drivers of phytoplankton dynamics and was already applied to a lake dataset (Rolinski et al. 2007). In the heterogeneous environment of a river, phytoplankton can show strong temporal changes on the short-term scale, like irregular fluctuations, seasonal variations and oscillations. Therefore, long-term observations are necessary to reveal the overlaying trends.

In the longitudinal profile, phytoplankton densities are variable and the prevailing phytoplankton biomass at a certain point in the river is the result of import, river-internal production and loss rates (e.g. due to grazing). In many running waters, benthic filter feeders, such as bivalves, can have a strong effect on the pelagic community and can exert a strong grazing pressure on phytoplankton (Cohen et al. 1984; Caraco et al. 1997).

The large central European rivers Rhine and Elbe provide good conditions for phytoplankton development due to the long residence time of the water. Both rivers are highly turbulent, fast flowing and are considered to be eutrophic, phytoplankton-rich rivers (river classification according to Behrendt and Opitz (2001)). Concerning the chlorophyll development in the Rhine, it was pointed out that the 1970s and 1980s were times of higher trophy, while during the last decade the development of a lower trophic state was observed (Friedrich and Pohlmann 2009). In the lower Rhine at Bimmen (Rhine-km 865), the mean chlorophyll *a* content during the growing season decreased from 59 µg L^{-1} in 1979 to 21 µg L^{-1} in 2004 (Friedrich and Pohlmann 2009). In contrast, the Elbe exhibits a high yield of chlorophyll *a* per unit total phosphorus (TP) (Mischke et al. 2011). At Schnackenburg (Elbe-km 475), mean chlorophyll *a* values of the growing season frequently surpassed 100 µg L^{-1} from 2000 to 2009 (data from the River Basin Community Elbe – RBC Elbe). In the Rhine catchment, wastewater treatment has been improved since 1970 (Friedrich and Pohlmann 2009) and in the Elbe, wastewater treatment improved and industrial effluents were reduced after the German reunification in 1989 (Adams et al. 1996). Despite these improvements, nowadays, ortho-phosphate (orthoP) concentrations in both rivers are still distinctly above the level which limits phytoplankton growth.

The mechanisms behind the large between-river differences in the phytoplankton development despite comparable nutrient concentrations in the Rhine and the Elbe are still unknown. One key question of this study is therefore how the chlorophyll *a* content and the occurrence of the spring bloom have changed over the last two decades in response to changing environmental conditions. The aim was to identify the most important physicochemical (meteorological, hydrological or chemical) variables that potentially govern the timing of the phytoplankton spring bloom and to test the main hypothesis that discharge decline during springtime is the prominent controlling factor. Therefore, long-term data of chlorophyll *a* and abiotic parameters from the Elbe (1994 – 2009, measuring station Magdeburg) and from the Rhine (1990 – 2009, measuring station Koblenz) were statistically analyzed (Chapter 2). Data from the measuring station Magdeburg (Elbe-km 312) were derived from the RBC Elbe and data from the measuring station Koblenz (Rhine-km 590) were derived from the Federal Institute of Hydrology (BfG).

The longitudinal plankton dynamics in relation to the production and loss processes prevailing during downstream transport were studied by means of four Lagrangian sampling campaigns

performed along the Rhine and the Elbe during different seasons (Chapter 3). These field investigations had a duration of 8 – 10 days according to the flow-time of the water and covered the impounded and free-flowing German part of the Rhine (Rhine-km 170 to 854) and the free-flowing German part of the Elbe (Elbe-km 0 to 582) including major tributaries. Besides phyto- and zooplankton, samples for the determination of nutrient, seston and oxygen concentrations as well as abundances of bivalves were analyzed. The main hypothesis was that higher net phytoplankton increases, i.e. rates of biomass change along the river, lead to higher chlorophyll concentrations in the downstream reaches of the Elbe compared to the Rhine.

Having considered the long-term trends of phytoplankton biomass during the last two decades and their present spatial dynamics in the longitudinal profile, the next question focused on the future development with respect to climate change. According to several studies, in European freshwater ecosystems, the occurrence of extreme meteorological conditions, like increased precipitation in winter or heat waves in summer, will probably increase in the context of climate change (Schär et al. 2004; Stott et al. 2004; Euro-limpacs 2008). Higher precipitation may for instance induce the probability of flood events leading to altered sediment budgets and changes in the amount of suspended substances. High amounts of suspended substances and high flow conditions worsen the average light conditions in the water column due to stronger light absorption and raised water-levels. Low light conditions in combination with reduced water residence times of the water during higher flows are negatively effecting the phytoplankton growth potential (Reynolds 2000). Salmaso and Zignin (2010), for instance, confirmed a negative effect of high discharge on phytoplankton development due to reduced water residence times in the lowland course of a highly flushed large river in Northern Italy. On the other hand, less precipitation in combination with lower discharge conditions and longer water residence time may stimulate algal growth (Admiraal et al. 1994; Reynolds and Descy 1996). The emission of green-house gases increased global surface temperature during the last 100 years by about 0.74 ± 0.18°C and global mean temperature is expected to increase between 1.4 – 5.8°C until 2100 (Wigley and Raper 2001; IPCC 2007). As stream temperature tracks air temperature (Langan et al. 2001; Mouthon and Daufresne 2006), the river water temperature is expected to increase in line with climate change. The response of temperate zone aquatic ecosystems to global warming is diverse and includes shifts in the geographic species distribution, biomass responses to warming, changes in biodiversity or shifts in biotic

interactions (Sommer et al. 2012). If other resources (light and nutrients) do not limit phytoplankton growth, higher water temperatures enhance phytoplankton growth (Reynolds 1984). But as light is often the limiting factor, the question arises if temperature has a prominent role in phytoplankton regulation. To assess the impact of climate change on water quality, dynamic, mechanistic models are an adequate tool, because they take into account the interactions of different processes (De Angelis and Mooij 2003; Ellner and Guckenheimer 2006).

Within this study, the main hypothesis concerning possible future states of the Rhine ecosystem is that climate change induced increases in water temperature and decreases in discharge conditions will enhance phytoplankton biomass. Therefore, a model for the majority of the free-flowing part of the Rhine (Rhine-km 359 to 865.5) was established using QSim, a deterministic, one dimensional water quality simulation model (Schöl et. al 1999). Through the modular structure of the model it is possible to represent different processes, for instance the plankton development, the oxygen balance, and the water temperature development using different climatological and hydrological input data. The model included the major tributaries as well as thermal discharges from industrial facilities (ICPR 2006, BUND 2009). To analyze the impact of climate change on the water quality (especially phytoplankton, oxygen and water temperature) in the Rhine, representative model chains were chosen from a model assemblage consisting of 30 combinations of global and regional climate models based on different CO_2 emission scenarios (IPCC 2007). The selected climate model chains were used to perform water quality simulations by means of the established model area for the Rhine (Chapter 4).

The present thesis includes a comparative analysis of phytoplankton long-term trends in relation to abiotic variables which provides a look upon predominating regulation mechanisms in the two rivers from a broader perspective. A detailed investigation of the spatial dynamics during downstream transport enhances the understanding of short-term fluctuations in plankton amounts and completes the analysis of important regulation processes. The knowledge obtained by evaluating the relevant driving forces helps to assess potential consequences of climate change on phytoplankton dynamics. A modeling approach elucidates the interaction of these different factors in the scope of climate change and allows to verify the newly acquired knowledge on phytoplankton regulation mechanisms.

2 What regulates the phytoplankton dynamics in large rivers? A comparative analysis of long-term data from the rivers Rhine and Elbe

2.1 Abstract

Knowledge about mechanisms and physical factors that control plankton dynamics in river ecosystems is essential for predicting future developments, e.g. in response to global climate change. The present study investigates long-term trends in phytoplankton biomass and shifts in the timing of phytoplankton spring blooms observed in the large rivers Rhine and Elbe from 1990 – 2009 and 1994 – 2009, respectively, and analyzes the factors regulating phytoplankton biomass. While phytoplankton biomass in the Elbe was high (seasonal mean chlorophyll *a* concentration: 62 µg L^{-1}) and did not show any long-term trend, it was much lower in the Rhine (seasonal mean chlorophyll *a* concentration: 10 µg L^{-1}) and has decreased significantly during the study period. This decrease coincided with an earlier occurrence of the phytoplankton spring maximum. In the Elbe, the analysis revealed that the timing of low discharge conditions was crucial for the occurrence of the spring bloom, i.e. an earlier end of the discharge maximum was connected with an earlier spring bloom. In the Rhine, there was a positive correlation between the timing of the spring bloom and the end of winter flood flow. The maximum chlorophyll *a* values during the bloom correlated with the timing of maximum light availability, which means that earlier occurrence of high light intensities was followed by lower maxima of spring bloom biomass. The findings indicate that climate related factors, like discharge or light conditions, have a high potential to regulate phytoplankton spring bloom dynamics. Such a dependence could be utilized for predicting phytoplankton development under climate change.

2.2 Introduction

Phytoplankton is a key component of river ecosystems, where it is often the dominant primary producer. It has been demonstrated that native populations of phytoplankton can evolve in large rivers, despite the loss of lotic phytoplankton downstream and despite stronger light attenuation in turbid rivers (Reynolds 1988; Dokulil 1994; Rojo et al. 1994). While plankton

dynamics have been studied extensively in lentic fresh waters such as lakes and reservoirs, comparatively little research has focused on factors that regulate phytoplankton biomass in lotic waters (Basu and Pick 1995; Reynolds 2000) and there is no general agreement concerning the factors that regulate phytoplankton growth in rivers (Reynolds 2000) compared with lakes (e.g. the PEG-model by Sommer et al. 1986). As phytoplankton dynamics respond quickly to local weather conditions and changes in discharge, it can be used as an indicator for changes in ecosystem functions in response to environmental change, including climate warming (Reynolds 1998).

Possible factors regulating the plankton dynamics in rivers may be physical (temperature, light), hydrological (discharge, water residence time), chemical (nutrient concentrations), and biotic (grazing, competition) (Reynolds 1988; Basu and Pick 1997; Bukaveckas et al. 2011). Sunlight is the most common limiting factor for primary production in streams (Basu and Pick 1996). Hydrological conditions prevailing in rivers strongly influence phytoplankton dynamics, for instance short residence times (Soballe and Kimmel 1987) or turbulence (Reynolds 1994). Both, light climate (via turbidity and water depth) and water residence time in rivers are ultimately controlled by discharge. Changing discharge may be an indirect effect of climate change acting on phytoplankton dynamics via altered snow melt and altered precipitation, which may affect biomass dilution, particle input (changing light climate) and nutrient input. Nutrient concentrations are mostly high in rivers affected by urbanization and agriculture and thus do rarely limit plankton growth in these systems (Reynolds and Descy 1996). Among other anthropogenic factors that potentially alter phytoplankton are wastewater treatment effluents and the heat emission by cooling water (Friedrich and Pohlmann 2009). Besides physical, hydrological, and chemical factors, biological factors like grazers can massively interfere with phytoplankton populations in rivers (Welker and Walz 1998; Schöl et al. 1999; Reckendorfer et al. 2006). All these different physicochemical, abiotic and biotic factors are known to alter phytoplankton dynamics in rivers. However, it is insufficiently known how these individual factors act in concert, and how phytoplankton responds to changes in these factors. Furthermore, studies on the effect of climatic conditions on phytoplankton growth in rivers are still rare (Gomes and Miranda 2001; Phlips et al. 2010; Ďesortová and Punčochář 2011).

Especially in spring, varying meteorological conditions are characteristic for the temperate climate region, and they are independent of developments during the preceding winter

(Rocznik 1995). It is of major importance to identify the factors that provoke changes in the occurrence and the magnitude of the spring bloom in rivers, because phytoplankton mass developments have a huge impact on water quality and ecosystem functions (Gallegos and Jordan 2002). The temporal occurrence of phytoplankton spring blooms in rivers may be highly variable and is yet difficult to predict (Admiraal et al. 1994). It can be assumed that in spring, the biological variables strongly depend on the rapidly changing environmental factors. Thus, the analysis of long-term trends, including the appropriate detection of cardinal dates during spring blooms, is a useful tool to identify relevant drivers of phytoplankton dynamics (Rolinski et al. 2007).

The large central European rivers Rhine and Elbe provide good conditions for phytoplankton development due to the long residence time of the water in both rivers. In the downstream reaches, the density of river plankton is generally highest (Vannote et al. 1980), due to longer retention times. The rivers Rhine and Elbe are highly turbulent, fast flowing and are considered to be eutrophic, phytoplankton-rich rivers (river classification according to Behrendt and Opitz (2001)). Following measures against eutrophication, like banning of phosphorus in detergents and the tertiary treatment of wastewater or reducing the inputs from agriculture, the trophic state of rivers and freshwaters was generally improved (Bloch 2001; Grizzetti et al. 2012). More recently however, the Rhine was reassigned to be a river with a low yield of chlorophyll *a* per unit total phosphorus (TP), whereas the Elbe was still among the rivers with a high yield of chlorophyll *a* per unit TP despite similar ranges of TP concentrations in both rivers (Mischke et al. 2011). Both rivers experienced increases in the water temperature in recent years together with an overall increase in air temperatures in central Europe (Belz and Gratzki 2009; Kysely 2010). Furthermore, the discharge of the Rhine changed, as it is influenced by snowmelt in the Alps during spring and early summer. In the Rhine, at Koblenz and Kaub, the Pardé coefficients (Pardé 1947) of mean monthly discharge from February to July during the last decade (2002 – 2011) decreased significantly compared to the preceding decade (1992 – 2001) (data provided by the BfG). In contrast, in the Elbe at Magdeburg the Pardé coefficients of mean monthly discharge from March to July revealed only small decreases (no significant changes) during recent years (2002-2011) compared with the preceding decade (1992 – 2001).

The present study analyzes long-term data for the development of phytoplankton biomass in the rivers Rhine and Elbe. The key question is how the chlorophyll *a* content and the

occurrence of the spring bloom have changed over time in response to changing environmental conditions. The aim of the study is to detect trends in the phytoplankton biomass and to identify the most important physicochemical (meteorological, hydrological or chemical) variables that potentially govern the timing of phytoplankton development in both rivers. The following hypotheses on the regulation of river plankton and on the effects of climate change are tested:

i) Environmental changes result in unidirectional trends in the long-term development of the phytoplankton biomass in both rivers.

ii) The timing of discharge decline is a prominent factor controlling the initiation and magnitude of the spring phytoplankton bloom in rivers.

iii) The timing of the phytoplankton bloom correlates with climate-related factors (i.e., temperature and discharge) in both large rivers regardless of their contrasting trophic state.

2.3 Methods

Study sites

The Rhine has its source in the Swiss Alps. It flows through Lake Constance (Rhine-km 0) and, further downstream, forms the border between France and Germany in the canalized part of the Upper-Rhine. The Rhine drains 185,260 km^2 in total, has a total length of 1,250 kilometer and a long-term mean annual discharge of 2,300 $m^3 s^{-1}$ at the end of the Lower Rhine, close to Emmerich (Germany) at Rhine-km 852 (Uehlinger et al. 2009). The main tributaries, which are important sources of phytoplankton, are the rivers Neckar, Main and Moselle (Bergfeld et al. 2009). The measuring station Koblenz, the sampling site of the present study, is located closely upstream the river mouth of the Moselle at navigation kilometer (Rhine-km) 590 in the Middle Rhine, approximately in the middle of the free-flowing German river reach, from Rhine-km 336, at the Weir of Iffezheim, to Rhine-km 891, the weir near Driel in the Netherlands. Concerning the chlorophyll development in the Rhine, the 1970s and 1980s were times of higher trophy, while subsequently the development of a lower trophic state was observed (Friedrich and Pohlmann 2009). At the measuring station Bimmen (Rhine-km 865), vegetation (March 1st to October 31st) chlorophyll *a* mean values were 59 µg L^{-1} in 1979 and decreased to about 21 µg L^{-1} in 2004, which still compares to

eutrophic conditions in lakes (Friedrich and Pohlmann 2009). Since the beginning of the 1990s, the anthropogenic inputs of nutrients have decreased.

The Elbe originates in the Czech Republic and has a catchment area of 148,268 km^2 and a total length of 1,094 km (ICPER 2005; Pusch et al. 2009). The free-flowing part of the Elbe begins 38 km upstream of the Czech-German border with the German navigation kilometer (Elbe-km) 0 (367 km from the source) and extends to Elbe-km 586 at the Weir of Geesthacht. The mean annual discharge at the Geesthacht Weir is 728 $m^3 s^{-1}$ (ICPER 2005). The most important tributaries along this reach are the rivers Mulde, Saale, and Havel. The water quality measuring station Magdeburg, the sampling site of the present study, is located at Elbe-km 312, approximately in the middle of the free-flowing river reach. Despite reduced nutrient inputs, high phytoplankton concentrations can still be observed in the Elbe, and chlorophyll measurements revealed that maximum chlorophyll concentrations regularly reached 200 µg L^{-1} and more at the end of the free-flowing section of the river (Guhr et al. 2004; Quiel et al. 2011).

Data origin and acquisition

From the station Koblenz (Rhine), weekly measurements of chlorophyll *a*, water temperature, TP content, and suspended substances (German Standard Methods DEW, 2007a) of the years 1990 – 2009 were used. Daily data of discharge and water-levels were taken from the upstream gauging station Kaub (Rhine-km 546) and converted to the station Koblenz (data from the Federal Waterways and Shipping Administration – WSV, provided by the BfG). The daily global radiation data originated from the meteorological station Geisenheim, located 70 kilometers south of Koblenz (49°98'N, 7°95'E) and were provided by the German Weather Service (DWD).

From the station Magdeburg (Elbe) data of chlorophyll *a*, water temperature, TP content, and suspended substances (German Standard Methods DEW, 2007a) from 1994 to 2009, measured at biweekly intervals were used (data provided by the RBC Elbe). The hydrological data for discharge and water-level on a daily basis originated from the gauging station Magdeburg (data from the WSV). The daily data of global radiation were derived from the weather station Magdeburg (52°06'N, 11°35'E) of the DWD.

Trend and peak analysis

Trend analyses of the phytoplankton biomass (chlorophyll *a*) were performed with different variables derived from a peak analysis and with mean chlorophyll concentrations (mean over the vegetation period from March to October). For peak analysis, so-called 'cardinal dates' in the time series were identified using a method proposed by Rolinski et al. (2007). The 'cardinal dates' describe the timing of the start point, the mid point, and the end point of a peak in days of the year, which are identified by means of fitting a Weibull-type function. By Rolinski et al. (2007), the method was applied to analyze a lake dataset, but the method is applicable to data sets from other water bodies as well. The advantage of the method is the identification of characteristic peaks and the corresponding dates from a diffuse array of sampling data points in an objectified way. The Weibull function smoothes measuring errors, and neighboring values are taken into account. It is thus appropriate to use the described method instead of choosing a certain threshold level or defining the week when maximal abundances occur in spring, which is commonly applied to determine the timing of phytoplankton spring peaks (Gerten and Adrian 2000). When more than one peak appears in the data set, the method serves to accomplish a peak comparison relative to the baseline, and only one peak is identified (Rolinski et al. 2007). By means of this peak analysis, the dates of the start point (S), the mid point (M), and the end point (E) of the spring phytoplankton peak of each year were identified. In the year 2009, no spring peak could be identified in the Rhine, because chlorophyll values were too low. The variables derived from the peak analysis as well as the mean chlorophyll concentrations (mean over the vegetation period) were then used for a trend analysis by means of the Mann-Kendall Test. This is a non-parametric, rank-based test for statistically significant trends in data series, wherein tests for significant monotonous trends over time, relying on Kendall's correlation coefficient, are performed (Yue and Wang 2004).

Calculation of light availability

The light availability was calculated using the Lambert-Beer law connecting the absorption of light with the characteristics of the medium. The photosynthetically active radiation (PAR) prevailing in the water column was calculated under consideration of global radiation, suspended substances, chlorophyll *a* concentration, and water depth (eq. 1 – 3; V. Kirchesch

unpubl.). As the water-level of a gauging station refers to a gauge zero point, each water-level value was corrected for the 'real' water depth identified in the profile.

The PAR in the water (I, µE m^{-2} s^{-1}) was calculated using the PAR at the water surface (I_0, µE m^{-2} s^{-1}), the extinction coefficient (ε) and the water depth (H, m) with the following equation:

$$I = \frac{I_0}{(\varepsilon \times H) \times (1 - \exp(-\varepsilon \times H))} \quad \textbf{(Eq. 1)}$$

The water depth (H) was calculated using water-level data on each sampling day. PAR at the water surface (I_0, µE m^{-2} s^{-1}) was calculated using available weather data of global radiation on each sampling day (GR, J cm^{-2} d^{-1}), the time of the day with sunlight (t_{light}, h d^{-1}) as well as a reflection factor (rf) of 0.97 and a conversion factor (cf) of 5.846 (1 J cm^{-2} h^{-1} = 5.846 µE m^{-2} s^{-1}, Harris 1978):

$$I_0 = \frac{GR}{t_{light}} \times rf \times cf \quad \textbf{(Eq. 2)}$$

The extinction coefficient (ε, m^{-1}) was calculated empirically using water quality data, i.e. the content of suspended substances (SS, mg L^{-1}) with a corresponding absorption coefficient of 0.13 (L m^{-1} mg^{-1}) and the chlorophyll *a* concentration (Chla, µg L^{-1}) with the corresponding absorption coefficient of 0.012 (L m^{-1} μg^{-1}) and a Chla:Biomass ratio of 21.5 (µgChla $mgBio^{-1}$) (Geider 1987), as well as a constant value for humic substances (hs) of 0.48 (m^{-1}):

$$\varepsilon = 0.13 \times (SS - \tfrac{Chla}{21.5}) + 0.012 \times Chla + hs \quad \textbf{(Eq. 3)}$$

Multivariate analysis of data

To test the relationship between the variables related to the phytoplankton spring bloom with physical, climatic and chemical variables, a multivariate analysis of the data was performed. The following dependent variables that describe the phytoplankton spring bloom were included (see section 'Trend and peak analysis'): start (S), mid (M) and end (E) of the spring

bloom peak in days of the year, the maximum value of the measured chlorophyll *a* in µg L^{-1} during the phytoplankton bloom (Max), the integral beneath the Weibull function as a proxy for total mass of the phytoplankton bloom in µg L^{-1} (Int) and the total duration of the bloom in days calculated by subtracting the day of the start of the bloom from the day of the end of the bloom (Dur).

The independent variables encompassed the TP content, date of maximum light availability (Light_M) (see section 'Calculation of light availability'), the day when water temperature exceeded 10°C (T10) and 12°C (T12), and the date of mid (Q_M) and end (Q_E) of the discharge peak. The TP content was calculated as the mean value of two weeks before the day of the beginning of the spring bloom. For the calculated light availability (Eq. 1) the peaks were determined according to Rolinski et al. (2007) as described for chlorophyll *a* before, and only the date of maximal light availability, i.e. the timing of light peak maximum was included in the following analysis. For the discharge data series, the peak determination was performed similarly and only the dates of the mid and the end of the peak were included, because particular attention was paid to the decline of the discharge with regard to spring bloom occurrence. As data for suspended substances, which were required for the calculation of the light availability, were not available from the years 1990 and 1991, the analysis of the Rhine dataset begins 1992.

A redundancy analysis (RDA) was performed to identify potentially important control factors. Subsequently, using the previous RDA result, the significance of environmental variables was assessed by the envfit function (Oksanen 2011). In the following multiple linear regression analysis, all different independent physicochemical variables, which potentially influence the phytoplankton development, were included. The variables were chosen using a stepwise backward selection, and only the variables which showed a significant effect were used in the subsequent analysis of variance (ANOVA). By means of the ANOVA, the effects of the selected independent variables on the dependent variables were analyzed. The R software (R Development Core Team 2010) was used for all computation and statistical analysis.

2.4 Results

The mean concentration of TP in the Rhine from 1990 to 2009 was 0.19 mg L^{-1} and the total amount decreased from 0.31 mg L^{-1} (average in 1990) to 0.12 mg L^{-1} (average in 2009). The

TP concentration in the Elbe was in a similar range (mean of 1994 – 2009: 0.22 mg L^{-1}) and decreased from 0.28 mg L^{-1} (average in 1994) to 0.18 mg L^{-1} (average in 2009) (Fig. 2.1). In the Elbe, low orthoP concentrations coincided with a high phytoplankton biomass. The seasonal (March to October) mean chlorophyll *a* concentration in the Elbe was about six fold higher compared with concentrations in the Rhine. The seasonal (March to October) mean chlorophyll *a* content in the Rhine (Rhine-km 590) was 10 µg L^{-1} and maximum values reached 102 µg L^{-1} in the observed time period, while seasonal mean concentration in the Elbe (Elbe-km 312) was 62 µg L^{-1} and maximal chlorophyll *a* concentrations of 296 µg L^{-1} were observed (Fig. 2.1). A trend analysis of the seasonal mean chlorophyll *a* concentrations revealed a significant decrease in the Rhine from 22 µg L^{-1} in 1990 to 1 µg L^{-1} in 2009 (Mann-Kendall Test, m = - 0.870; $p < 0.001$) (Fig. 2.2a). At the same time, in the Elbe chlorophyll *a* values tended to increase from 52 µg L^{-1} in 1994 to 65 µg L^{-1} in 2009, but not significantly (Mann-Kendall Test, m = 1.556; $p = 0.096$) (Fig. 2.2b).

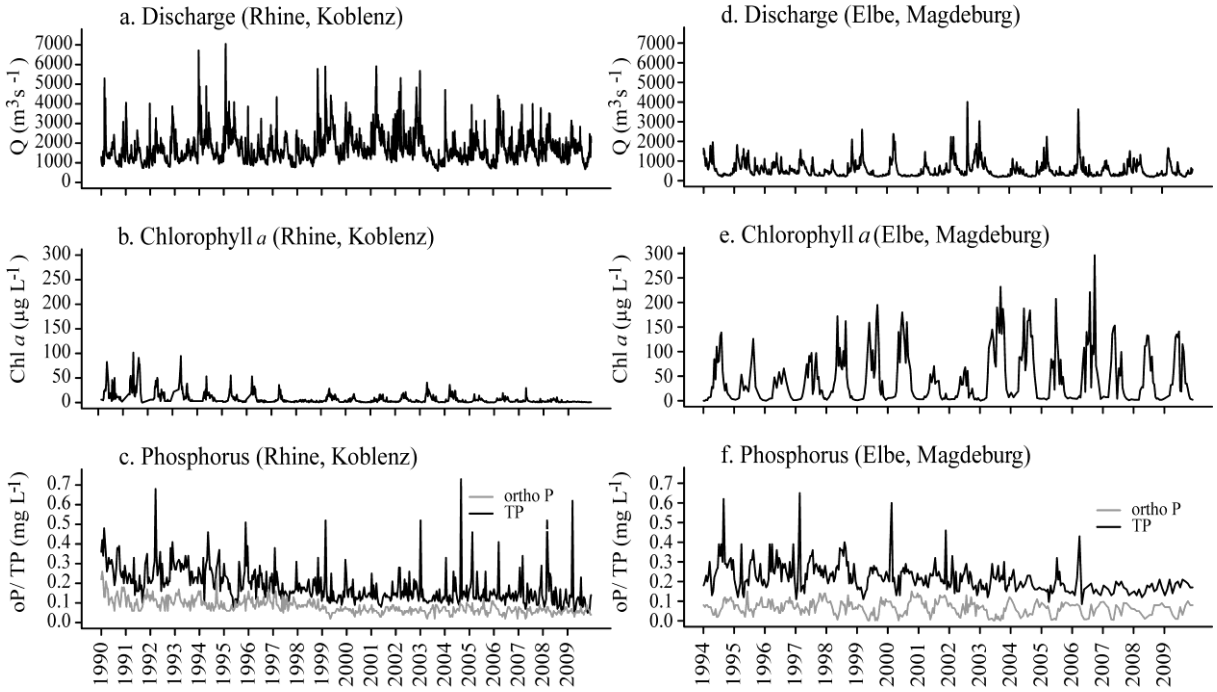

Fig. 2.1: Background data for (a, b, c) the Rhine at Koblenz from 1990 to 2009 and (d, e, f) the Elbe at Magdeburg from 1994 to 2009: (a, d) discharge, (b, e) chlorophyll *a* concentration and (c, f) TP and orthoP concentration.

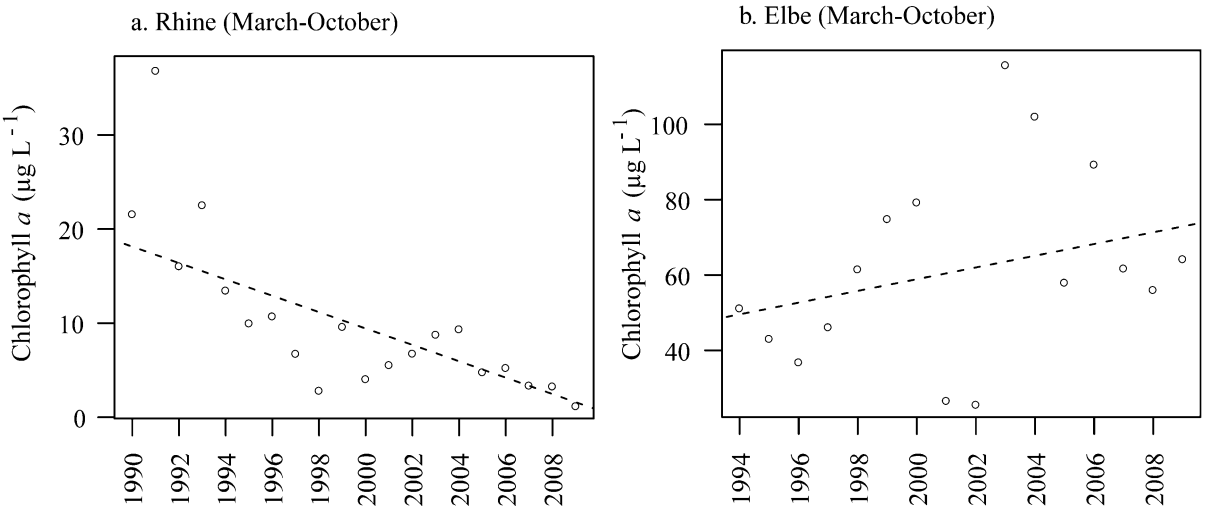

Fig. 2.2: Mean chlorophyll *a* concentration during the vegetation period March to October in (a) the Rhine at the station Koblenz from 1990 to 2009 and (b) the Elbe at Magdeburg from 1994 to 2009. Lines represent trends according to the Mann-Kendall Test with a slope of - 0.870 ($p < 0.001$) for the Rhine and of 1.556 ($p = 0.096$) for the Elbe.

The maximum of the spring bloom in the Rhine occurred increasingly earlier in the year during the time series 1990 – 2008, as demonstrated by a significant effect in the Mann-Kendall Test (m = - 2.461; $p = 0.009$) (Fig. 2.3a). At the beginning of the study period in 1990, it had occurred around day 132 (beginning of May) whereas the timing of the spring phytoplankton peak shifted towards end of March (day 83) in recent years. In contrast, the date of the maximum of the spring bloom showed no significant trend in the Elbe (Mann-Kendall Test, m = 0.177; $p = 0.343$) (Fig. 2.3b).

However, these recent early phytoplankton peaks in the Rhine were much smaller than the peaks recorded in the beginning of the study period. The chlorophyll *a* content in the Rhine at the time of the peak maximum decreased strongly in the years from 1990 to 2008 (Mann-Kendall Test, m = - 2.913; $p = 0.001$) (Fig. 2.4a). In the Elbe, there was a non-significant increase in chlorophyll *a* concentration at the time of peak maximum (Mann-Kendall Test: m = 3.499; $p = 0.112$) (Fig. 2.4b). This matches the observed trends in mean chlorophyll *a* concentration during the vegetation period (March – October), which also showed a strong and significant decline in the Rhine and a non-significant increase in the Elbe (Fig. 2.2).

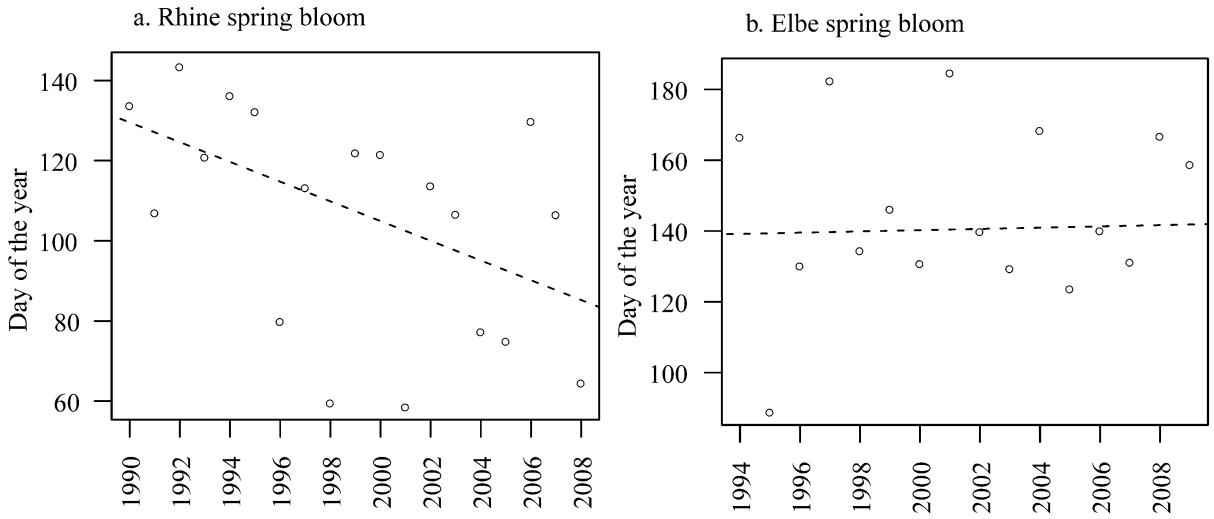

Fig. 2.3: Mid of the spring bloom peak in (a) the Rhine at Koblenz from 1990 to 2008 and (b) the Elbe at Magdeburg from 1994 to 2009. Lines represent trends according to the Mann-Kendall Test with a slope of - 2.461 (p = 0.009) for the Rhine and of 0.177 (p = 0.343) for the Elbe.

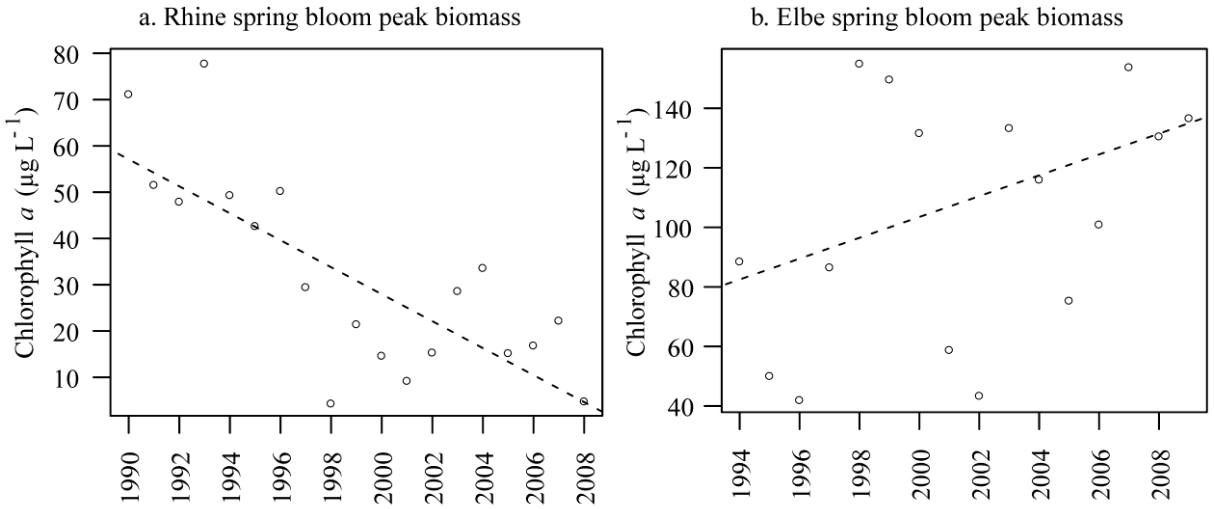

Fig. 2.4: Maximum chlorophyll *a* concentration during the spring bloom (a) in the Rhine at Koblenz (1990 – 2008) and (b) the Elbe at Magdeburg (1994 – 2009). Lines represent trends according to the Mann-Kendall Test with a slope of - 2.913 (p = 0.001) for the Rhine and of 3.499 (p = 0.112) for the Elbe.

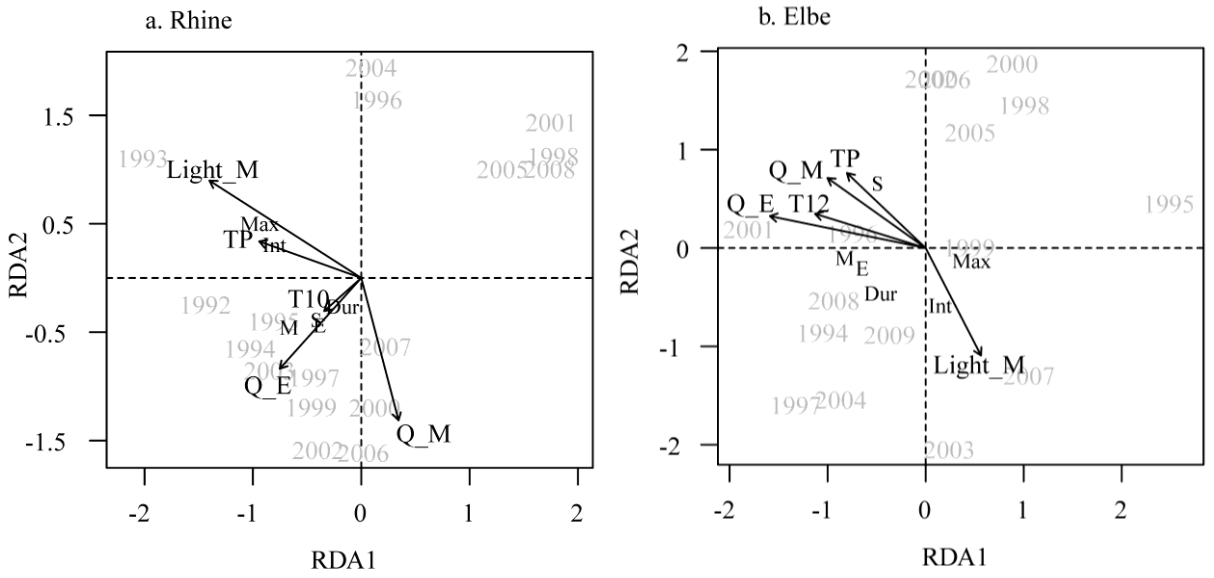

Fig. 2.5: First two axes of RDA with 'environmental factor analysis' of all dependent variables (small letters): start (S), mid (M), end (E), maximum value (Max), total mass (Int) and duration (Dur) of the spring bloom in (a) the Rhine at Koblenz from 1992 – 2008 and (b) the Elbe at Magdeburg from 1994 to 2009. Results of environmental factor analysis for the Rhine: maximum light availability (Light_M) $p = 0.009$; mid of the discharge peak (Q_M) $p = 0.063$; end of the discharge peak (Q_E) $p = 0.132$; water temperature exceeding 10°C (T10) $p = 0.752$ and total phosphorus (TP) $p = 0.198$. Results of environmental factor analysis for the Elbe: maximum light availability (Light_M) $p = 0.105$; mid of the discharge peak (Q_M) $p = 0.112$; end of the discharge peak (Q_E) $p = 0.016$; water temperature exceeding 12°C (T12) $p = 0.164$ and total phosphorus (TP) $p = 0.184$.

The RDA included all dependent variables concerning the phytoplankton bloom and all independent, i.e. physical and chemical variables (Fig. 2.5a). The subsequent environmental factor analysis performed with all variables indicated for the Rhine that the phytoplankton development (biomass and peak) was significantly related to the timing of maximum light availability (Light_M) and that the timing of discharge peak (Q_M) was also important. By contrast, the variables temperature and nutrient concentration had no effect. The multiple linear regression was performed to select the variables for the ANOVA. The results of the ANOVA confirmed that the timing of maximum light availability (Light_M) had a significant effect on the maximum of the chlorophyll *a* content during the bloom (Max; $p = 0.001$; $R^2 = 0.54$) (Table 2.1). The end of the discharge peak (Q_E) instead of mid discharge peak (Q_M) as revealed by the environmental factor analysis, was significantly related to the timing of the spring bloom peak (M) in the ANOVA (Q_E; $p = 0.029$), but the relationship

was rather weak (R^2 = 0.32) (Table 2.1). Like in the previous analyses, all other variables concerning water temperature and nutrient concentration had no significant effect on the phytoplankton spring bloom peak.

Table 2.1: Results of the ANOVA and the multiple linear regression analysis for the Rhine (Koblenz) for the response variables mid of the spring peak (M) and maximum chlorophyll *a* value during the spring peak (Max). The results of the ANOVA for the selected independent variables are presented and the result of the multiple linear regression including these independent variables (cf. section 2.3 Methods 'Multivariate analysis of data').

M (peak mid)					
ANOVA	Df	Sum Sq	Mean Sq	F value	*p*-value
Q_E	1	3792.7	3792.7	6.0307	0.029
Light_M	1	318.1	318.1	0.5059	0.490
Q_E:Light_M	1	609.9	609.9	0.9698	0.343
Residuals	13	8175.7	628.9		
REGRESSION	Df	Standard error	R-squared	F-statistic	*p*-value
	15	14.12	0.324	8.661	0.010
Max					
ANOVA	Df	Sum Sq	Mean Sq	F value	*p*-value
Light_M	1	2991.50	2991.50	15.7377	0.001
T10	1	559.07	559.07	2.9411	0.108
Residuals	14	2661.20	190.09		
REGRESSION	Df	Standard error	R-squared	F-statistic	*p*-value
	15	10.07	0.543	20.01	< 0.001

The patterns showed pronounced differences in the Elbe. The RDA and environmental factor analysis identified the end of the discharge peak (Q_E) to be important for the timing of the phytoplankton peak (Fig. 2.5b). This was confirmed by the ANOVA showing that the end of the discharge peak (Q_E) significantly influenced the timing of the spring bloom peak (M) (Q_E; p = 0.012; R^2 = 0.40) (Table 2.2). The variables concerning light condition, nutrient concentration, and water temperature had no significant effect in any of the performed analyses, and regarding the maximum value of the chlorophyll *a* content (Max), no significant effect of any factor could be identified.

Table 2.2: Results of the ANOVA and the multiple linear regression analysis for the Elbe (Magdeburg) for the response variables mid of the spring peak (M) and maximum chlorophyll *a* value during the spring peak (Max). The results of the ANOVA for the selected independent variables are presented and the result of the multiple linear regression including these independent variables (cf. section 2.3 Methods 'Multivariate analysis of data').

M (peak mid)					
ANOVA	Df	Sum Sq	Mean Sq	F value	*p*-value
Q_E	1	3337.6	3337.6	8.4099	0.012
T12	1	762.0	762.0	1.9200	0.189
Residuals	13	5159.3	396.9		
REGRESSION	Df	Standard error	R-squared	F-statistic	*p*-value
	14	12.77	0.40	11.12	0.005
Max					
ANOVA	Df	Sum Sq	Mean Sq	F value	*p*-value
TP	1	2193.5	2193.5	1.3801	0.260
Residuals	14	22252.2	1589.4		
REGRESSION	Df	Standard error	R-squared	F-statistic	*p*-value
	14	11.94	0.025	1.38	0.260

2.5 Discussion

The present study revealed contrasting, bidirectional trends concerning phytoplankton biomass in the rivers Rhine and Elbe, which indicates that the phenomena are river system specific and can differ regionally. In the two rivers, phytoplankton dynamics are subject to different regulation mechanisms, involving timing of discharge reduction and light availability. This indicates that controlling factors for phytoplankton growth in rivers clearly differ from the common regulation mechanisms for lacustrine plankton.

Contrasting trends in phytoplankton biomass development

No statistically significant long-term trend in phytoplankton biomass could be detected in the Elbe (station Magdeburg) with respect to mean chlorophyll *a* concentration, whereas the mean chlorophyll *a* concentration in the Rhine (station Koblenz) decreased significantly from 1990 to 2009 (hypothesis i). While the Rhine is characterized by a low chlorophyll *a*/TP ratio, this ratio is high in the Elbe (Mischke et al. 2011). Thus, in the Elbe, nutrients are effectively incorporated into phytoplankton biomass. This stands in contrast to the Rhine, where the significance of loss processes is strongly indicated. Both rivers have a high growth potential

for phytoplankton due to high nutrient concentrations. Phytoplankton densities and longitudinal increases in the Rhine were high in past years, indicating that strong net growth is potentially possible with respect to the river structure (Friedrich and Pohlmann 2009). However, more recent studies showed for phytoplankton only small, if any, net increases along the river (Scherwass et al. 2010). Furthermore, Weitere and Arndt (2002) demonstrated for heterotrophic flagellates, that the nanoplankton had high growth rates in the Rhine, which were not converted into increases along the river, i.e. significant losses of plankton occur within the Rhine. One possible reason for these losses in the Rhine are benthic filter feeders. In addition to *Dreissena polymorpha*, the invasive bivalve *Corbicula fluminea* has established in the Rhine since the 1990s and reached high abundances (Friedrich and Pohlmann 2009).

In general, variations in flow and retention times in rivers can control the trophic relationships in the plankton (Admiraal et al. 1994), and in the Rhine, low flows and high water temperatures are associated with stronger interaction of plankton and benthic filter feeders (Weitere and Arndt 2002; Viergutz et al. 2007). Thus, during periods of low flow, the strength of the bentho-pelagic coupling or the effect of grazing on phytoplankton may increase, leading to indirect effects of the flow conditions on the plankton abundance. In the Elbe, high TP concentrations coincide with high concentrations of chlorophyll, but no long-term trend in the biomass could be detected in the present study (station Magdeburg). The high phytoplankton concentrations in the Elbe can partly be explained by high inputs from the impoundments of the upper Elbe, high nutrient concentrations, a favorable light climate, and long residence times (Quiel et al. 2011). Despite low inputs from the Upper Rhine, the Rhine is provided by supplementary phytoplankton inputs due to impoundments in the tributaries. Plankton reduction via benthic filter feeding is low in the Elbe due to generally low abundances of bivalves. Taking these different control mechanisms in the two rivers, together with the contrasting trends (towards distinctly earlier timing of the spring peak and reduced biomass in Rhine; weak effects in the Elbe), it appears likely that the loss processes rather than the growth processes are subject to temporal trends.

Phytoplankton losses to zooplankton are generally low in the Rhine due to very low abundances of both metazooplankton and algivorous protozoans (Weitere et al. 2005). Such losses to the zooplankton are temporarily important in the Elbe. However, this appears particularly in reaches below the sampling site of the present study (Holst et al. 2002). It

appears thus unlikely that the dynamics of the phytoplankton are altered by the zooplankton at both study sites.

The hydrological regime rather than temperature triggers the spring bloom

In the first hypothesis, the decrease of the spring discharge peak was proposed to be the most important regulating factor (hypothesis ii). The results of the present study showed that the discharge decrease partly controlled the spring increase in phytoplankton in the Rhine, and the timing of decreasing discharge explained the timing of maximum spring biomass in the Elbe. Increasing retention times during low discharge conditions generally improve the conditions for the development of planktonic organisms, particularly by increasing the light availability (decreasing turbidity and water depths) and the prolonged water residence time (Reynolds 1995; Lucas et al. 2009). Especially in spring, low discharge conditions can promote high phytoplankton development, as observed in the Elbe. In the Rhine, timing of maximum light availability significantly correlated with maximal chlorophyll values during the bloom in the present study. In contrast to lakes, where temperature associated to stratification is frequently highlighted as controlling factor of phytoplankton development, the present study could not confirm the importance of water temperature for large rivers. Likewise, in the present study, no significant effect was found of the timing of water temperature increase on phytoplankton spring bloom dynamics, whereas the timing of discharge reduction could be identified to be the crucial climatic factor.

Implications for future development

Besides discharge, prevailing nutrient concentrations may strongly correlate with river phytoplankton biomass (Basu and Pick 1996; Van Nieuwenhuyse and Jones 1996). In the present study, however, TP concentration had only a minor influence on the timing of phytoplankton mass development and could not be related to temporal trends in phyto-plankton spring development. In the Rhine catchment, wastewater treatment has been improved since 1970 (Friedrich and Pohlmann 2009) and in the Elbe, wastewater treatment improved and industrial effluents were reduced after the German reunification in 1989 (Adams et al. 1996). In the Elbe, orthoP levels decreased from 0.26 mg PO_4-P L^{-1} in 1990 to 0.07 mg PO_4-P L^{-1} in 2000 (Guhr and Schwartz 2006). In the Rhine, phosphorus was reduced

from 0.65 mg PO_4-P L^{-1} in 1970 to 0.11 mg PO_4-P L^{-1} in 2004 (Friedrich and Pohlmann 2009). Thus, after these improvements, orthoP concentrations in both rivers were still distinctly above the level which limits phytoplankton growth and the long-term decline in orthoP concentrations alone is therefore an unlikely reason for the drastic decline in chlorophyll *a* concentrations in the Rhine. Nutrient concentrations set the upper limit for phytoplankton biomass. This biomass threshold can at times be reached in the Elbe, where favorable growth conditions in terms of light and water residence time prevail.

The results of the present study underline the assumption that nutrient concentrations are sufficient for phytoplankton growth, and that the hydrological factors water residence time and discharge dynamics predominantly govern the phytoplankton dynamics in many large rivers. Due to the dominant effect of flow conditions, a change in spring flow should lead to a temporal shift of the phytoplankton bloom (hypothesis iii). Accordingly, the results of the present study revealed that the maximum of the spring bloom in the Rhine appears earlier and can be connected with a change in the discharge conditions, whereas in the Elbe the timing of the spring bloom did not show any significant trend.

Several studies predict changes in the discharge regimes of rivers due to climate change (Weiland et al. 2012). For the Rhine, projections of a multi-model approach indicate a reduction of discharge in summer for the 'far future' (2071 – 2100; Nilson et al. 2010b). For the Elbe, water quality modeling suggests that climate change could lead to longitudinal shifts in primary production and respiration due to changes in discharge conditions (Quiel et al. 2011). The findings of the present study suggest that among changing climatic conditions, particularly changes in precipitation and cloud cover have the potential to alter phytoplankton spring bloom dynamics and to superimpose other river system specific properties, for instance nutrient availability. In contrast to lakes, where temperature triggers stratification, increases in water temperature might have a weaker impact on riverine phytoplankton. Furthermore, the present data suggest that the anticipated climate change might have contrasting effects in the rivers under study. In systems with complex regulation mechanisms such as grazing by benthic filter feeders, changes in flow or water temperature can interact in multiple ways with the food web regulation. In contrast, systems, in which phytoplankton is predominantly controlled by nutrient concentrations, probably respond less pronounced towards climatic changes and nutrient management might be an effective means to control climate change effects. Finally, systems, in which phytoplankton is regulated mostly by flow, such as the

Elbe or many impounded rivers, may be directly effected by future changes of flow conditions.

3 Longitudinal plankton dynamics in the rivers Rhine and Elbe

3.1 Abstract

The present study investigates the influence of hydrological, physical, and chemical factors acting on planktonic organisms (phyto- and zooplankton) during downstream transport in two large rivers. Therefore, four Lagrangian sampling campaigns were performed along the entire German part of the impounded and free-flowing river reaches of the river Rhine (Rhine-km 170 to 854) in September 2010 and May 2011 and along the complete free-flowing, German part of the river Elbe (Elbe-km 4 to 582) in September 2009 and August 2011. This approach allowed to focus on prevailing longitudinal dynamics and to investigate spatio-temporal patterns. Low chlorophyll concentrations could be observed in the Rhine (maximal values below 5 µg L^{-1} in 2010), in contrast to high concentrations in the Elbe (maximal values of 174 µg L^{-1} in 2009 and 123 µg L^{-1} in 2011). Higher densities of benthic filter feeders in the Rhine, could potentially explain the differences in phytoplankton biomass. An exceptional extreme event with unusually high chlorophyll values exceeding the concentrations in the Elbe was observed in May 2011 in the Rhine (maximal values of 244 µg L^{-1}). This phenomenon demonstrated that at times of favorable low discharge conditions and high light intensities, strong phytoplankton increases can temporarily lead to a pronounced regime shift. Tributaries represented an additional and important source of phytoplankton biomass and suspended substances in the Rhine, whereas they primarily diluted the plankton amounts in the Elbe. In particular, the findings of the present study demonstrated that phytoplankton biomass in the lower river reaches is a result of the conditions prevailing during downstream transport, irrespective of the start values in the upper river reaches.

3.2 Introduction

Plankton dynamics in large rivers

Lentic environments are complex and dynamic habitats with great temporal and spatial variability. In large rivers, planktonic organisms are subjected to a well mixed, turbulent water column, to changing flow regimes and variable water residence times. They can only increase in abundance if they are capable of a sufficient ratio of increase to compensate for

advective losses. High reproduction rates typical for small organisms, for instance protozoa or, among the metazooplankton, rotifers, are beneficial (Viroux 1997; Reckendorfer et al. 1999; Lair 2006). In large rivers, internal primary production derived from phytoplankton is a main source of organic substance for organisms on higher trophic levels (Thorp and Delong 1994; Thorp and Delong 2002). Phytoplankton is thus a central element in large river food webs. In addition, it affects the oxygen budget of the river system.

Phytoplankton growth and regulation mechanisms in large rivers

For the phytoplankton production in rivers, especially the retention time of the water, connected to the discharge conditions is very important. In large, fast flowing and turbulent rivers changing discharge conditions affect light climate (via water depth and turbidity), particle input, and water residence time which is important with regard to generation times of planktonic organisms. Although it is a combination of different factors that govern phytoplankton development, sometimes single dominant factors can be identified (cf. Chapter 2). For instance, irradiance was crucial for phytoplankton biomass in the estuary of the river Rhine (Kromkamp et al. 1995). The importance of connectivity with backwaters and regulation for phytoplankton growth in rivers was highlighted in several studies (Reynolds 1995; Wehr and Thorp 1997). The highly turbulent flow conditions in large river systems create a well-mixed water column without gradients in, for instance, water temperature or nutrient concentrations. Concerning the chemical factor, nutrient concentrations can temporarily limit phytoplankton growth in summer, but they are usually present in sufficient concentrations in the Rhine and the Elbe (Ietswaart 1999; Quiel et al. 2011). Apart from physical factors, biotic factors can massively interfere with phytoplankton populations and community structure, exerting a top-down effect (Vitousek et al. 1996; Welker and Walz 1998). In most running waters, benthic filter feeders, such as bivalves, can have a strong effect on the pelagic community and exert a strong grazing pressure on phytoplankton (Cohen et al. 1984; Caraco et al. 1997).

Chlorophyll concentrations, a comparison between Rhine and Elbe

In large rivers, autotrophic primary production by phytoplankton is next to direct organic inputs from the riparian zone a major energy source supporting communities of higher trophic

levels (Thorp and Delong 1994). The conditions for phytoplankton growth in the Rhine and the Elbe are favorable, because residence time of the water is long enough to allow phytoplankton growth. Inoculation of phytoplankton is mediated by lakes or dam-regulated regions in the upper parts or by impoundments in the tributaries. In the free-flowing part of the Rhine, phytoplankton densities are influenced by the import from the major tributaries Neckar, Main and Moselle which are characterized by numerous impoundments and high plankton concentrations (Uehlinger et al. 2009). A similar situation and high plankton concentrations are found in nearly all of the tributaries of the Elbe (for instance Saar and Havel) and a constant inoculation of phytoplankton is provided from the impoundments in the Czech section, the upper part of the Elbe (Pusch et al. 2009).

The Rhine is a river with a high specific run-off and is characterized by a low yield of chlorophyll *a* per unit total phosphorus (TP), whereas the Elbe has a low specific run-off and a high yield of chlorophyll *a* per unit TP (Mischke et al. 2011). Maximal chlorophyll concentrations at the measuring station Koblenz (Rhine-km 590) reached 102 µg L^{-1} during the time span 1990 – 2009 and the mean of the vegetation period (March to October) was 10 µg L^{-1} for this time period (data from the Federal Institute of Hydrology – BfG, International Commission for the Protection of the Rhine – ICPR, cf. Chapter 2). Furthermore in the Rhine at Bimmen (Rhine-km 865), the mean chlorophyll *a* value of the growing season was observed to decrease, as it was determined to be 59 µg L^{-1} in 1979 and 21 µg L^{-1} in 2004 (Friedrich and Pohlmann 2009). In 1989, a maximal chlorophyll *a* concentration of 170 µg L^{-1} was measured during the peak of a phytoplankton bloom (Friedrich and Pohlmann 2009). By contrast, in the Elbe a maximum of 296 µg L^{-1} was reached during the time span 1994 – 2009 at the measuring station Magdeburg (Elbe-km 312) and the mean of the vegetation period was 62 µg L^{-1} (cf. Chapter 2). At Schnackenburg (Elbe-km 475), mean chlorophyll *a* values during the growing season were even higher and frequently surpassed 100 µg L^{-1} from 2000 to 2009 (data from the River Basin Community Elbe – RBC Elbe). Therefore, overall lower chlorophyll *a* values in the Rhine were expected during the sampling campaigns compared to the Elbe.

Longitudinal plankton dynamics in Rhine and Elbe

According to the longitudinal development of chlorophyll concentrations, a downstream increase in plankton abundance is characteristic for the large rivers Rhine and Elbe. As for the

abiotic parameters, the well mixed and turbulent water conditions inhibit the formation of gradients in phyto- and zooplankton distribution in both rivers. In the Rhine, a pronounced decrease in phyto- and zooplankton abundance during the last decades was documented (Friedrich and Pohlmann 2009), and recently a relatively low phytoplankton biomass was observed in the Rhine (Weitere et al. 2005; Scherwass et al. 2010). In the Elbe by contrast, high phytoplankton biomasses were typically observed and concerning phytoplankton composition, diatoms accounted for the majority of the total biomass (Guhr et al. 2004). Likewise, in the lower part of the Rhine, diatoms dominated phytoplankton communities (De Ruyter van Steveninck et al. 1990; Scherwass et al. 2010), probably due to high surface to volume ratios of small centric diatoms and high growth rates in turbulent and turbid conditions (Reynolds and Descy 1996).

Typical for river plankton is the dominance of small taxa in phyto- and zooplankton communities due to their shorter generation time and their ability to reproduce fast when water retention times are short. Therefore, concerning zooplankton composition, rotifers are often dominating zooplankton populations in diverse river systems including Rhine and Elbe (Admiraal et al. 1994; Holst et al. 2001).

Focus of the present study

In order to analyze differences in phytoplankton composition and dynamics of algal biomass in rivers, longitudinal profiles in the form of Lagrangian sampling campaigns are a useful tool, i.e. following a water parcel traveling downstream. Therefore, an estimate of the flow time of the water is necessary. This downstream transport of water can be calculated with a hydraulic model relying on current daily measurements of water discharges (De Ruyter van Steveninck et al. 1992). As a Lagrangian sampling campaign involves a high logistic effort and the use of research vessels or small boats, only few studies of this kind have been realized so far (Köhler 1997; Lair and Reyes-Marchant 1997; Ietswaart et al. 1999; Scherwass et al. 2010). Studies investigating the longitudinal dynamics of river plankton mainly focused on a single river system (Bahnwart et al. 1998; Welker and Walz 1998; Viroux 2002).

In the present study, the two large rivers Rhine and Elbe were investigated by means of several Lagrangian sampling campaigns in order to connect longitudinal changes in physical parameters and nutrient concentrations to changes in plankton abundance and biomass. The

motivation was to test whether changes in environmental factors are reflected by comparable changes in plankton dynamics in time and space and to relate phytoplankton abundances in lower reaches to upstream dynamics. As phytoplankton development strongly depends on different environmental factors, physical parameters like water temperature and under water light climate as well as chemical parameters like nutrient concentrations, these parameters were measured additionally to the plankton sampling. Net changes of phytoplankton along the river were considered, including river-internal growth and loss processes on the one hand and the 'external' impact of tributaries on the other hand. The rate of change in phytoplankton biovolume between two sampling sites along the free-flowing part of the river was calculated as the 'net increase', because loss processes like sedimentation or grazing were included.

The benthic filter-feeding bivalves *Dreissena polymorpha* and *Corbicula fluminea* are neozoan species in the Rhine, originating from the Black Sea and Asia (Araujo et al. 1993). Since 1970, *Dreissena polymorpha* has spread out in the Rhine, subsequent to water quality improvements. *Corbicula fluminea* has invaded the Rhine since 1990 and is present in high abundances nowadays (Friedrich and Pohlmann 2009), exerting a strong grazing impact on phytoplankton. It is one hypothesis, that the low present phytoplankton densities in the Rhine are a consequence of high grazing pressures of the invasive bivalves in the Rhine in contrast to the Elbe. However, systematic comparative studies are as yet lacking. To consider these potential grazing impacts, size distribution of benthic filter feeding bivalves in the Rhine was recorded for the year 2010 and abundance for the year 2011 in the Rhine and in the Elbe (data from the BfG, provided by Franz Schöll).

Two Lagrangian sampling campaigns were performed along the Rhine from the Swiss-German border along the upper, canalized section followed by the free-flowing lower part to the Dutch-German border, in September 2010 and in May 2011. Likewise, in the German part of the Elbe, two Lagrangian sampling campaigns were realized along the free-flowing section from the Czech-German border to the Weir of Geesthacht in September 2009 and August 2011. The results of the four Lagrangian sampling campaigns were analyzed together and comparisons were made in order to elucidate spatio-temporal patterns in plankton during longitudinal transport.

The performance of these longitudinal sampling campaigns served to test the following hypotheses:

i) Higher chlorophyll concentrations in the middle and low reaches of the Elbe in comparison to the Rhine are a result of higher within-river net phytoplankton increases in the free-flowing part of the Elbe rather than of higher import from dam-influenced upper reaches.

ii) Tributaries have the potential to alter longitudinal phyto- and zooplankton developments in the Rhine and the Elbe.

iii) Differences in the net plankton increase between the two rivers can potentially be explained by different densities of benthic filter feeders.

3.3 Methods

The spatial dynamics in plankton, suspended substances, nutrients and physical parameters were followed downstream along the Rhine in autumn 2010 (September 21st – September 29th) and spring 2011 (May 17th – May 27th) and along the Elbe in autumn 2009 (September 4th – September 13th) and summer 2011 (August 8th – August 15th). Sampling was conducted in a Lagrangian approach, i.e. in the longitudinal river profile, with the sampling sites being chosen according to the flow time of the water (Fig. 3.1). In 2010 and 2011, samples were taken at 18 and 21 locations, respectively in the Rhine and at 6 and 8 locations, respectively in its tributaries and backwaters. In 2009 and 2011, samples were taken at 10 and 8 locations, respectively in the Elbe and at 4 locations in the most important tributaries.

Study sites

The Rhine, one of the largest rivers in central Europe has a catchment area of 185,260 km^2, a total length of about 1,250 km and a long-term mean discharge (MQ) of 2,300 m^3 s^{-1} at the Dutch-German border at Rhine-km 865 (Uehlinger et al. 2009; see Fig. 3.1). The Rhine-km provided here are used for navigation and are counted from the outlet of Lake Constance. In the so-called Upper Rhine from Rhine-km 170 to Rhine-km 336, 90 % of the water flows in a parallel canal equipped with 10 impoundments. This artificial canal has a mean water depth of 9 to 11 m. The middle and lower sections between Rhine-km 336 and Rhine-km 854 flows freely with a mean water depth of 3 – 5 m. In the present study, the section between Rhine-km

170, close to Basel, and Rhine-km 865, close to Bimmen, was investigated. The mean residence time of the water from Rhine-km 170 to 865 is approximately 8 days and the MQ is 1,060 $m^3 s^{-1}$ at Rhine-km 170 (data from the WSV, provided by the BfG). The most important tributaries in the free-flowing section are the Neckar, the Main, and the Moselle. The trophic state of the Rhine is moderately eutrophic (Friedrich and Pohlmann 2009). The concentration of river plankton increases in the course of the Rhine, owing to the long residence time of the water (Bergfeld et al. 2011).

The Elbe has a catchment area of 148,268 km^2 and a total length of 1,094 km (Pusch et al. 2009). The upper part of the Elbe includes 24 impoundments. The Elbe-km provided here are counted starting at the Czech-German border, 367 km downstream from the source of the Elbe. The longitudinal survey encompassed the free-flowing stretch of the Elbe from the Czech-German border (Elbe-km 0) to the tidal weir at the city of Geesthacht (Elbe-km 586). The MQ is 353 $m^3 s^{-1}$ at Hrensko, (Elbe-km 0), and 728 $m^3 s^{-1}$ at the Geesthacht Weir (Elbe-km 586). At MQ, the water depth in the middle Elbe is 3 – 4 m. Important tributaries in this section are the Mulde, the Saale and the Havel. The average water transport time at MQ is about 8 days from Elbe-km 0 to Elbe-km 586. The Elbe is a highly eutrophic river with pronounced phytoplankton blooms during spring and summer.

Sampling in the Rhine

In both sampling campaigns along the Rhine a river reach of 674 km length was sampled (from Rhine-km 170 to 854), including both, the canalized and the free-flowing section. The same water parcel was followed downstream using different research vessels. Between Rhine-km 170 (Basel) and Rhine-km 590 (Koblenz), samples were taken from the Research Vessel ‘Max Honsell’, belonging to the ‘LUBW’ (Landesanstalt für Umwelt, Messungen und Naturschutz Baden-Württemberg). From Rhine-km 590 (Koblenz) to Rhine-km 854 (Bimmen), the sampling was performed from the ‘Max Prüss’, the Research Vessel belonging to the ‘LANUV NRW’ (Landesamt für Natur, Umwelt und Verbraucherschutz Nordrhein-Westfalen). A hydraulic transport model, the Alarm-model, was used for the calculation of downstream water transport time. The Alarm-model was originally developed for predictions of arrival and propagation of hazardous substances in the Rhine and has the potential to predict measured water transport times with an accuracy of 1 to 4 % (Spreafico and Mazijk 1993). All water discharge information used for the modeling were derived from the WSV

and were provided by the BfG. Samples of surface water were taken directly from research vessels in the middle of the river and at about 30 m distance from the left and right river bank at every sampling station with a 10 liter bucket. The samples were prepared on board of the ships which were equipped with laboratories. Additionally, measuring probes were installed on board of the ships in a continuous flow measuring box. The box was connected to a pump and provided with fresh river water from below the ship in a constant discharge flow-through.

Sampling in the Elbe

In both sampling campaigns along the Elbe, a 578 km river reach from Schmilka (Elbe-km 4) to Geesthacht (last sampling station at Elbe-km 582) was sampled. Samples were taken from a small motor-boat with a bucket; additionally, physicochemical variables were measured with multi-probes (Yellow Spring Instruments, Inc.). The flow time of the river water was calculated with the hydrodynamic model Hydrax (Oppermann 1989). Hydrax is based on a morphological model of the corresponding river system and calculations are performed with real time input data. Samples were taken in the middle of the river and at the left and right river bank within 15 – 20 minutes from the motor-boat. Samples were prepared in a mobile laboratory (laboratory bus), providing all the necessary instruments, measuring and filtering devices. For the presentation of the results, the three samples (one from the middle, one from the left and one from the right side) were averaged.

Sampling procedure and analysis of the samples

At each sampling station, O_2 and water temperature were measured in situ by means of multiple probes (Yellow Spring Instruments, Inc.). For the determination of phytoplankton, unfiltered water samples were preserved with Lugol's solution (0.5 %) and stored in 250 ml brown glass bottles at room temperature until analysis. For collecting zooplankton in sufficient numbers, 10 – 20 liters of water were filtered through a plankton net (mesh size 55 µm), concentrated in a 50 ml bottle and fixed with formaldehyde (4 %). Phytoplankton and zooplankton species were counted and species were identified down to the lowest possible taxonomic level. Phytoplankton and zooplankton cells were counted and measured to obtain abundance, biovolumes, and dry weight (German Standard Methods DIN, 2006).

The analysis of nutrients and suspended substances was carried out using German Standard Methods (German Standard Methods DEW, 2007b). For measuring the seston content, i.e. the amount of total suspended substances, up to 3 liters of the river water (depending on the concentration of particles) were filtered via vacuum filtration and using glass fiber filters (Whatman GF/F, 100 mm). The filters were pre-weighted and stored in small cups for later analysis in the laboratory where the filters were dried at 100°C in a drying furnace for 24 hours and weighed to obtain the dry weight of seston. From the remaining filtrate of the seston processing, 30 ml of river water were filtered using a filter syringe (0.45 µm) and put into the freezer for measurement of the dissolved silicate. Another 30 ml of the filtrate were filtered through a filter syringe (0.45 µm) and stored in a glass bottle for later nutrient analysis, i.e. ortho-phosphate (orthoP), nitrate, and ammonium. For the analysis of total organic carbon, an unfiltered water sample was fixed with HCl and stored in the deep-freezer. To measure the chlorophyll content, 1 – 2 liters of the river water were filtered through glass fiber filters (Whatman GF/F, 50 mm), and the filters were cut into pieces, extracted in hot 80 % ethanol and stored in brown glass bottles. Later, the determination of the chlorophyll *a* content was performed according to German Standard Methods (DEW, 2007b). With the sample from the middle of the river, chlorophyll *a* content was additionally determined by HPLC-technique. Therefore, 1 – 2 liters of the water sample were filtered through glass fiber filters (Whatman GF/F, 50 mm) and the filters were put in PE-tubes and quick-frozen in liquid nitrogen. At selected stations, light attenuation under water was measured using a spherical sensor (LI-COR LI-1400). The sensor measured the photosynthetically active radiation (PAR, radiation in the range of wavelengths between 400 and 720 nm) and was lowered gradually from the water surface to the maximal possible depth. The compensation depth, commonly used to define the euphotic zone (Reynolds 2006), is the depth at which light reaches 1 % of its surface value and was calculated by exponentially fitting the measured light values on a logarithmic scale against water depth.

Determination of net phytoplankton increase between two sampling sites

The rate of change in phytoplankton biovolume was determined in situ along a free-flowing river reach without tributary influence. This net increase in biovolume between two sampling sites included losses to grazers and sedimentation.

To calculate the net rate of increase and the doubling time, the following equations were used:

$$r\ (net\ rate\ of\ increase\ along\ the\ river) = \frac{(\ln T_2 - \ln T_1)}{t}$$

T_2 = mean total phytoplankton biovolume ($mm^3\ L^{-1}$) at sampling site 2
T_1 = mean total phytoplankton biovolume ($mm^3\ L^{-1}$) at sampling site 1
t = flow time between sampling site 1 and 2 (days)

$$d\ (doubling\ time\ along\ the\ river) = \frac{\ln(2)}{r} = \frac{0.69}{r}$$

Bivalve abundance in Rhine and Elbe

For 2011, results of a sampling campaign performed along the channel floor of the Rhine and the Elbe for inventory control of the macrozoobenthos are presented. These samplings are annually performed by the BfG in the scope of a measuring campaign which was routinely carried out since 1986 in the Rhine (Schöll 2009) and since 1992 in the Elbe (Schöll and Balzer 1998). In 2011, 122 samples were taken along the Rhine from Rhine-km 170 to 850 (Rhine-km 170 to 360: 18/04/11 – 21/04/11; Rhine-km 360 to 850: 16/05/11 – 24/05/11) and 105 samples along the Elbe from Elbe-km 4 to 580 (Elbe-km 4 to 255: 07/06/11 – 09/06/11; Elbe-km 255 to 580: 28/06/11 – 30/06/11). At each sampling site, samples were taken from the right side, the middle and the left side of the river. The samples collected to determine bivalve abundance (*Corbicula* sp. und *Dreissena* sp.) during the sampling campaign in the Rhine performed in May 2010 from Rhine-km 168 to 850 (03/05/2010 – 19/05/2010) were further analyzed. In addition to the bivalve abundance per m^2, the shell length of the bivalves from all 200 samples taken between Rheinfelden (Rhine-km 170) and Bimmen (Rhine-km 865) was determined.

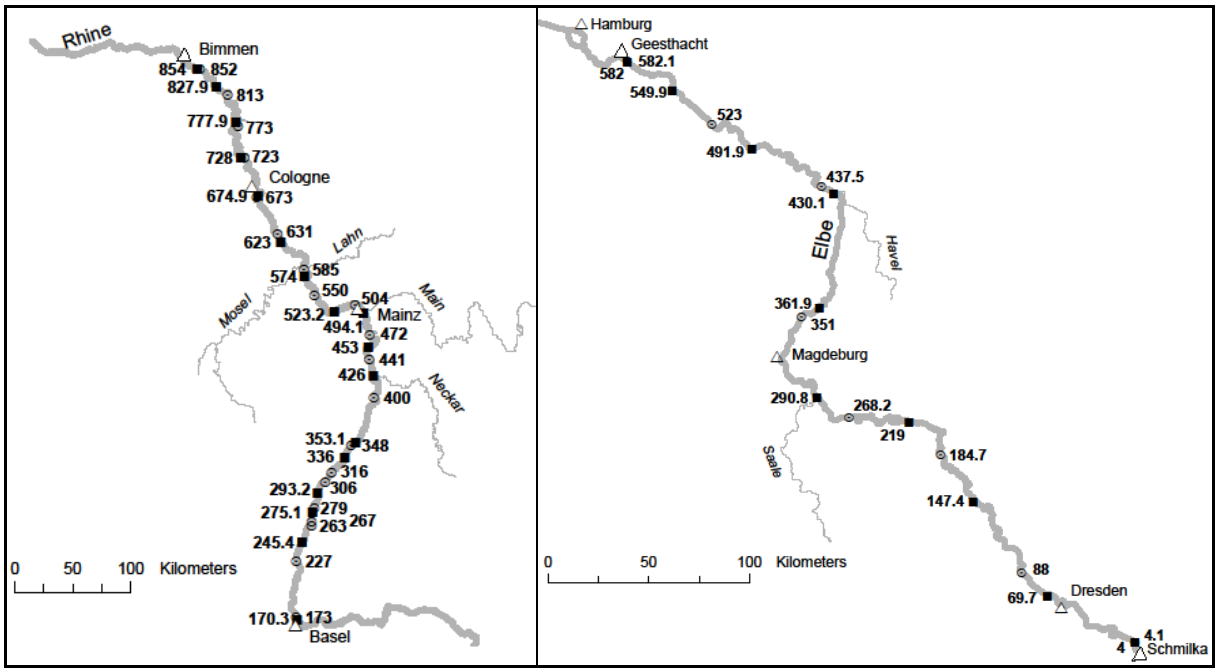

Fig. 3.1: Sampling sites Rhine (left) with 18 sampling stations in 2010 (left side of the river, squares) and 21 sampling stations in 2011 (right side of the river, circles). Sampling sites Elbe (right) with 10 sampling sites in 2009 (left side of the river, squares) and 8 sampling stations in 2011 (right side of the river, circles).

3.4 Results

Development of water quality parameters

In the Rhine, the Lagrangian sampling campaign in September 2010 was characterized by an intermediate discharge situation (Q_{Bimmen} = 1,730 m^3 L^{-1}), whereas the discharge in May 2011 was lower (Q_{Bimmen} = 1,030 m^3 L^{-1}) (Table 3.1). This was also reflected in the flow time of the river water which was only 8 days (198 h) in September 2010 and 10 days (238 h) in May 2011. The compensation depth for light was deeper than the mean water depth in September 2010, except for the last station close to Bimmen (Rhine-km 854) in 2010. In 2011, compensation depth was generally lower, particularly at the station below the confluence of the Main (Table 3.1).

At the beginning of the campaign, at Rhine-km 170, all nutrient concentrations except orthoP were higher in May compared to September (Table 3.1). Total phosphorus and total nitrogen concentration increased downstream. The orthoP concentration and the Si concentration

increased along the river stretch investigated in September, but both dissolved nutrients strongly decreased in May. Mean orthoP concentration was 0.06 mg L^{-1} in September and 0.03 mg L^{-1} in May. While nitrate-N concentrations increased to 2.1 mg L^{-1} from the start point Basel to the end point Bimmen in September, they showed no clear pattern in May and decreased slightly from the beginning (Rhine-km 173) to the end of the survey (Rhine-km 852). Ammonium-N was present in very low concentrations throughout the entire sampling campaign in September. In May, the ammonium-N concentrations were about an order of magnitude higher.

Seston values in the Rhine in September 2010 were 8.8 mg L^{-1} and increased up to a maximal value of 16.6 mg L^{-1} at the end point of the survey (Rhine-km 854), congruent to total organic carbon (TOC) concentrations. Despite similar start concentrations, in May 2011, there was a stronger increase in seston concentration and at the end of the investigated river reach at Rhine-km 852, seston concentration amounted to 54.4 mg L^{-1}. Likewise, TOC concentrations increased to 5.7 mg L^{-1} in 2011, in contrast to lower concentrations of 3.7 mg L^{-1} in 2010 (Rhine-km 854).

In the main tributaries in September, all nutrient concentrations were permanently higher or equal to the concentrations in the main river (Table 3.1). The river Lahn showed remarkably high seston values of 24.6 mg L^{-1}. In May, the dissolved silicate content in the tributaries was lower compared to the main river. All tributaries were characterized by higher seston and TOC concentrations compared to the Rhine.

In the Elbe, the discharge was low in September 2009 ($Q_{Geesthacht}$ = 257 m^3 s^{-1}), while in August 2011 the discharge was higher ($Q_{Geesthacht}$ = 738 m^3 s^{-1}) (Table 3.2). Compensation depth was roughly equal to the mean water depth, only in the lowest river reaches, compensation depth was lower than the mean water depth.

The nutrient concentrations orthoP, nitrate-N, ammonium-N, and Si, generally decreased downstream in both surveys, except for nitrate-N in August 2011. The mean orthoP concentration was 0.07 mg L^{-1} in September and 0.09 mg L^{-1} in August. TOC and seston content increased along the investigated river reach in both years.

Table 3.1: Discharge and nutrient development at selected stations along the Rhine in autumn 2010 and spring 2011 during the Lagrangian sampling campaigns from Rhine-km 170 to 854. Travel time = water travel time (h), Q = discharge (m^3 s^{-1}), WT = water temperature (°C), TP*/TN = total phosphorus/nitrogen (mg L^{-1}), PO_4-P* = orthoP (mg L^{-1}), NO_3-N = nitrate-N (mg L^{-1}), NH_4-N = ammonium-N (mg L^{-1}), SiO_2-Si = dissolved silicate-Si (mg L^{-1}), TOC = total organic carbon (mg L^{-1}), D = mean water depth in the cross-sectional profile (m); LCD = light compensation depth (1 % surface light) (m). * In 2011, TP and orthoP were corrected with measuring values from the ICPR, because during the measurement an error occurred.

Rhine autumn 2010 (September 21st – September 29th)							**Tributaries**			
Kilometer; travel time (location)	170; 0 (Basel)	353; 71 (Karls-ruhe)	494; 107 (Mainz)	574; 131 (Koblenz)	674;155 (Köln)	854; 198 (Bimmen)	Neckar (km 428)	Main (km 496)	Lahn (km 585)	Mosel (km 595)
Q	938	938	1220	1250	1540	1730	53	148	23	151
WT	16.99	17.80	19.38	18.00	16.94	16.72	16.57	17.12	14.48	16.87
D; LCD	7; 7.7	4.6; 7.9	3.8; -	4.1; 6.5	4.0; 4.6	3.8; 3.2	-	-	-	-
TP	0.04	0.05	0.08	0.11	0.12	0.11	0.22	0.19	0.26	0.17
PO_4-P	0.03	0.03	0.06	0.07	0.08	0.09	0.19	0.18	0.20	0.16
TN	1.14	1.38	1.68	2.05	2.61	2.72	4.74	5.16	3.44	2.96
NO_3-N	0.88	0.99	1.26	1.72	1.87	2.11	4.21	4.39	2.78	2.47
NH_4-N	0.04	0.02	0.02	0.02	0.02	0.02	0.02	0.05	0.05	0.03
SiO_2-Si	0.83	1.14	1.47	1.81	2.22	2.27	2.99	4.25	5.86	2.93
TOC	1.90	3.40	4.00	3.00	3.20	3.70	4.10	5.80	6.70	5.30
Seston	8.84	5.08	10.24	11.64	10.47	16.55	9.87	13.17	24.60	6.60
Rhine spring 2011 (May 17th – May 27th)							**Tributaries**			
Kilometer; travel time (location)	173; 0 (Basel)	348; 95 (Karls-ruhe)	504; 143 (Mainz)	585; 167 (Koblenz)	673;191 (Köln)	852; 238 (Bimmen)	Neckar (km 428)	Main (km 496)	Lahn (km 585)	Mosel (km 595)
Q	721	647	898	888	1010	1030	61	118	12	45
WT	15.91	19.32	20.74	21.13	20.03	19.06	19.91	21.00	18.83	20.55
D; LCD	6.7; 8.4	3.9; 8.8	3.2; 2.8	2.8; 4.5	3.0; -	2.29; -	-	-	-	-
TP*	0.03	0.06	0.15	0.11	0.11	0.05	0.17	0.17	0.31	0.12
PO_4-P*	0.02	0.04	0.05	<0.05	<0.01	<0.01	0.04	0.03	0.08	<0.05
TN	1.63	1.73	2.98	2.48	2.33	2.68	4.08	4.57	2.56	2.10
NO_3-N	1.29	1.37	2.15	1.76	1.43	1.22	2.88	3.05	0.99	0.87
NH_4-N	0.15	0.12	0.12	0.10	0.11	0.13	0.13	0.15	0.11	0.12
SiO_2-Si	1.44	1.54	0.92	0.86	0.44	0.04	0.32	0.14	0.12	0.32
TOC	5.80	3.40	3.50	4.30	4.60	5.70	8.40	11.00	8.80	8.00
Seston	9.06	6.11	20.79	17.23	25.19	54.41	10.97	31.27	33.20	22.70

In the main tributaries of the Elbe, nitrate-N concentrations were low in September and did not exceed the concentration in the main river. In contrast, in May, the nitrate-N concentration was higher in all tributaries compared to the main river. The tributary Mulde had lower nutrient concentrations compared to the main river, while the river Havel was characterized by a very high orthoP concentration of 0.14 mg L^{-1} both, in September and in August. In September, tributary concentrations of seston did not exceed the seston concentration of the main river, in contrast the first two tributaries were characterized by very low seston concentrations in the range of only 3 mg L^{-1}. In August 2011, all tributaries clearly indicated lower seston concentrations compared to the main river. Thus, in contrast to the Rhine, the

tributaries exerted a diluting effect. The mean orthoP concentration was in the same range in both rivers, whereas the nitrate-N and Si concentrations were higher in the Elbe compared to the Rhine. It can be summarized that the nutrient development downstream the Elbe revealed decreasing concentrations for both surveys, whereas in the Rhine nutrient development proceeded in opposite directions: in September 2010 nutrient concentrations increased and in May 2011, nutrient concentrations decreased downstream. Concerning total nitrogen, mean concentration in the Rhine was 2.8 mg L^{-1} in contrast to 3.5 mg L^{-1} in the Elbe and mean TP concentration was 0.22 mg L^{-1} in the Rhine and 0.19 mg L^{-1} in the Elbe.

Table 3.2: Discharge and nutrient development at selected stations along the Elbe in autum 2009 and summer 2011 during the Lagrangian sampling campaigns from Elbe-km 4 to 582. Travel time = water travel time (h), Q = discharge (m^3 s^{-1}), WT = water temperature (°C), TP/TN = total phosphorus/nitrogen (mg L^{-1}), PO_4-P = orthoP (mg L^{-1}), NO_3-N = nitrate-N (mg L^{-1}), NH_4-N = ammonium-N (mg L^{-1}), SiO_2-Si = dissolved silicate-Si (mg L^{-1}), TOC = total organic carbon (mg L^{-1}), D = mean water depth in the cross-sectional profile (m); LCD = light compensation depth (1 % surface light) (m).

Elbe autumn 2009 (September 4th – September 13th)									**Tributaries**	
Kilometer; travel time (location)	4; 0 (Schmil-ka)	69; 24 (Dres-den)	147; 47 (Torgau)	361; 113 (Magde-burg)	430; 137 (Witten-berge)	582; 179 (Geest-hacht)	Schwarze Elster (km 198)	Mulde (km 260)	Saale (km 291)	Havel (km 438)
Q	138	143	155	232	270	270	6	23	42	28
WT	21.07	18.87	17.63	19.97	18.93	17.80	21.10	20.80	20.40	19.00
D; LCD	2.5; 2.3	2.3; -	2.9; 2.9	2.8; 2.7	2.4; -	2.2; 1.2	-	-	-	-
TP	0.19	0.19	0.18	0.18	0.15	0.15	0.05	0.19	0.18	0.31
PO_4-P	0.10	0.10	0.11	0.06	0.03	0.01	0.01	0.05	0.09	0.14
TN	3.46	3.55	3.57	3.29	3.34	2.72	1.16	3.27	4.21	1.65
NO_3-N	2.65	2.89	2.94	2.52	2.27	1.36	0.72	2.51	3.09	0.14
NH_4-N	0.08	0.06	0.05	0.05	0.05	0.06	0.03	0.04	0.05	0.06
SiO_2-Si	3.81	3.98	4.05	3.11	2.48	0.92	4.59	2.71	1.81	3.38
TOC	9.50	9.00	11.00	9.90	12.00	12.00	6.60	6.30	7.70	16.00
Seston	13.75	15.12	15.04	17.02	21.80	33.67	3.07	3.10	17.40	20.50
Elbe summer 2011 (August 8th – August 15th)									**Tributaries**	
Kilometer; travel time (location)	4; 0 (Schmil-ka)	46; 12 (Dres-den)	184; 42 (Torgau)	351; 89 (Magde-burg)	430; 113 (Witten-berge)	582; 153 (Geest-hacht)	Schwarze Elster (km 198)	Mulde (km 260)	Saale (km 291)	Havel (km 438)
Q	231	251	268	425	707	738	29	64	61	183
WT	20.95	19.58	18.79	18.90	19.68	19.19	17.51	18.02	19.44	18.91
D; LCD	3.0; -	3.0; -	3.7; -	3.7; -	4.0; 1.2	4.1; -	-	-	-	-
TP	0.20	0.21	0.21	0.20	0.21	0.22	0.12	0.14	0.19	0.22
PO_4-P	0.10	0.12	0.11	0.09	0.06	0.08	0.08	0.09	0.12	0.14
TN	3.89	4.52	4.24	3.96	4.56	3.04	2.93	4.20	5.63	2.84
NO_3-N	3.10	3.12	2.69	2.67	2.43	1.79	2.10	3.35	3.02	0.80
NH_4-N	0.03	0.02	0.03	0.03	0.03	0.03	0.07	0.06	0.05	0.05
SiO_2-Si	4.55	4.62	4.57	4.17	3.68	3.83	6.84	4.87	3.40	5.46
TOC	5.90	6.37	7.97	7.50	7.70	11.67	7.20	4.30	2.70	10.00
Seston	16.53	16.42	31.10	29.95	36.08	38.5	14.15	4	-	17.15

Oxygen and phytoplankton development

From the beginning until the end of both surveys in the Rhine, the oxygen saturation was permanently high, with almost 100 % saturation (Fig. 3.2a,b). The oxygen saturation values in the main tributaries Neckar, Main, Lahn and Moselle were approximately in the same range as in the main channel. In spring 2011, the oxygen saturation at the beginning of the survey (Rhine-km 173) was 92 %, and at the end of the survey, at Rhine-km 852, oxygen was supersaturated with 129 %. In contrast to 2010, all main tributaries showed extremely high oxygen saturation values, with a maximal value of 199 % in the river Main.

The oxygen saturation of the Elbe in September 2009 increased from 88 % at Elbe-km 4 up to 165 % downstream, which matches increasing chlorophyll *a* values (Fig. 3.2c,d; Fig. 3.3c,d). Oxygen saturation values of most of the tributaries were lower than in the Elbe itself. In August 2011, the oxygen saturation at Elbe-km 4 was 121 % and increased to 163 % at Elbe-km 438. Comparing the oxygen saturation values in the Rhine and Elbe, higher values during the sampling campaigns were reached in the Elbe. The tributaries of the Rhine mostly reached higher super-saturation values compared to the main stream, whereas almost all saturation values in the tributaries of the Elbe were lower than in the main stream.

The chlorophyll *a* concentration in the Rhine was characterized by seasonal and longitudinal heterogeneity. In September 2010, the chlorophyll *a* concentration in the Rhine was below 5 µg L^{-1}, and the phytoplankton biovolume approximately doubled on the way downstream (Fig. 3.3a; Fig. 3.4a). The chlorophyll concentration in the tributaries was in the range of that in the main river. Only in the Rest-Rhine (Rhine-km 291), the concentration exceeded the concentration in the main river with 7 µg L^{-1}. Likewise, the phytoplankton biovolumes ranged between 0.8 to 2 mm^3 L^{-1} in the Rhine and most tributaries showed equal or higher values compared to the main stream (Fig. 3.4a). In May 2011, the chlorophyll concentration at the start point of the survey, at Rhine-km 170, was similar to that in September 2010, but at the end of the survey chlorophyll *a* concentrations were much higher (Fig. 3.3b). The chlorophyll *a* values remained at a low level of about 2 µg L^{-1} until Rhine-km 400, where the free-flowing part of the river began, and increased steadily up to a value of 60 µg L^{-1} at Koblenz (Rhine-km 590) and to 244 µg L^{-1} chlorophyll *a* at Rhine-km 854, the last station of the survey. This is a 100-fold increase compared to the start values.

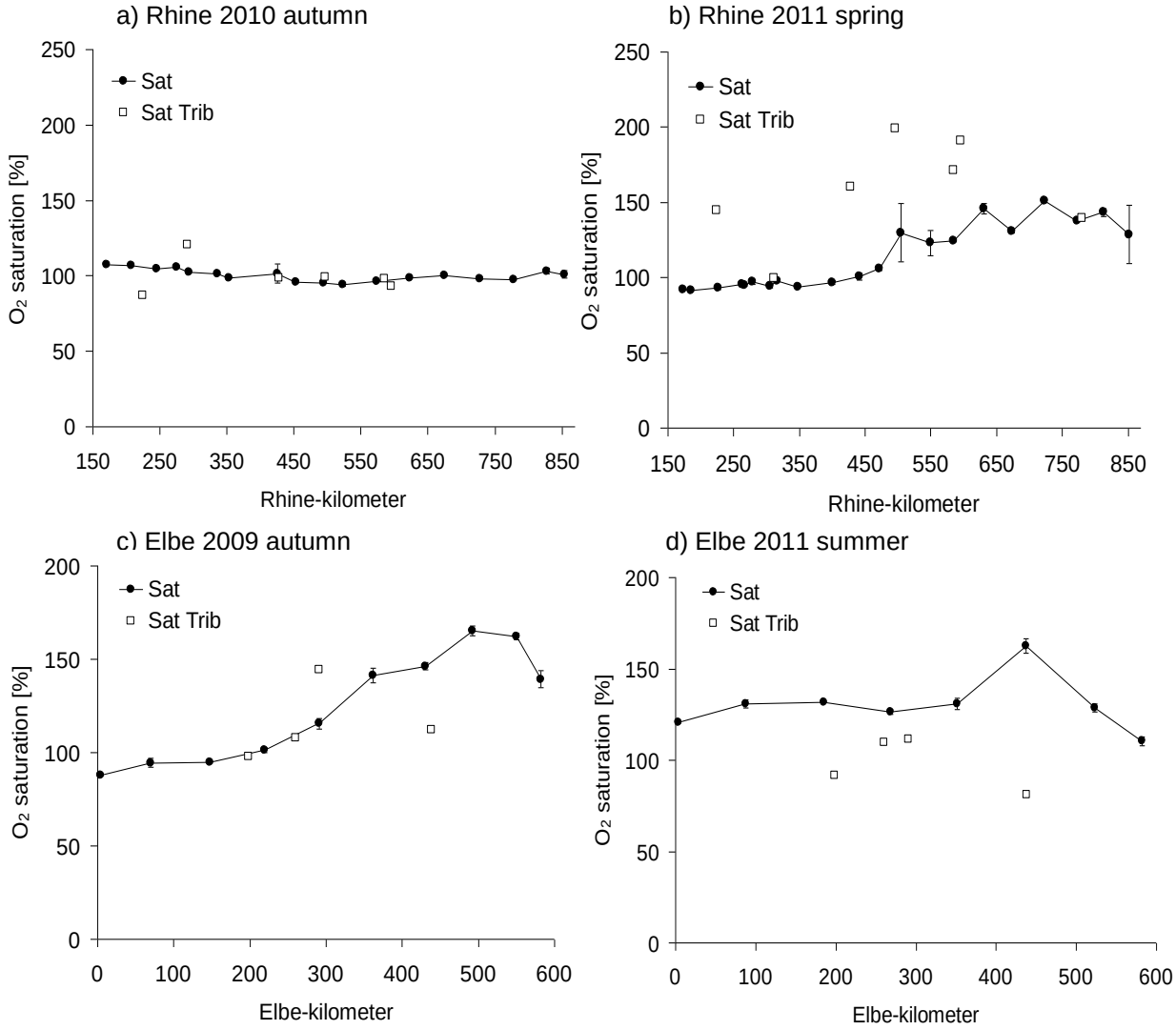

Fig. 3.2: Oxygen development presented as saturation during downstream transport in the Rhine in autumn 2010 (a) and spring 2011 (b) and in the Elbe in autumn 2009 (c) and summer 2011 (d). Filled symbols connected with a line present values of the main river as a mean of the samples collected from the left side, the right side, and the middle of the river, ± standard deviation. Empty symbols represent values of main tributaries or backwaters (a: Rest-Rhine km 225, Rest-Rhine km 291, Neckar, Main, Lahn, Moselle; b: Rest-Rhine km 225, Ill, Neckar, Main, Lahn, Moselle, Ruhr; c and d: Schwarze Elster, Mulde, Saale, Havel).

Likewise, the main tributaries situated along the free-flowing part of the Rhine, especially the Lahn, showed very high chlorophyll *a* values of up to 250 µg L^{-1}. Despite similar start values in September 2010 and May 2011, the phytoplankton biovolume was higher with maximal values exceeding 8 mm^3 L^{-1} in May 2011 (Fig. 3.4b). Like in 2010, the total phytoplankton biovolume in the tributaries Neckar, Main, Lahn, Moselle and Ruhr frequently surpassed the

values prevailing in the main stream. In contrast to chlorophyll values which were steadily increasing from Rhine-km 400 to 854, there was an abrupt increase in phytoplankton biovolumes at Rhine-km 400 to 440 (from 1.5 to 5.3 mm^3 L^{-1}). Within this river reach, the tributary Neckar (Rhine-km 428) had a high phytoplankton biovolume (7.0 mm^3 L^{-1}).

The chlorophyll *a* concentration in the Elbe in September 2009, increased from 6.5 µg L^{-1} to 174 µg L^{-1} which is a 27-fold increase from Elbe-km 4 to 582 (Fig. 3.3c). Phytoplankton biovolume increased from 4.5 mm^3 L^{-1} at Elbe-km 4 to 13.5 mm^3 L^{-1} at Elbe-km 582 (Fig. 3.4c). In contrast to the Rhine, where tributaries had mostly higher chlorophyll *a* values, all tributaries of the Elbe presented lower chlorophyll *a* concentrations and were diluting the phytoplankton concentrations of the main stream (Fig. 3.3c). Likewise, most tributaries contained lower phytoplankton biovolumes compared to the main river (Fig. 3.4c). In August 2011, chlorophyll *a* concentrations remained generally lower compared to 2009, despite a higher start concentration of 36 µg L^{-1} at Elbe-km 4 (Fig. 3.3d). Chlorophyll *a* concentration increased to a maximum of 123 µg L^{-1} at Elbe-km 582, which is a 4-fold increase. Standard deviations were high, indicating a pronounced lateral concentration difference, probably due to the influence of tributaries. Similar to September 2009, the tributaries had a diluting impact on the main stream, for instance the Havel showed only 16 µg L^{-1} chlorophyll *a*, while the Elbe carried more than 100 µg L^{-1} at this location. In 2011, the phytoplankton biovolume ranged between 7.4 and 9.4 mm^3 L^{-1} in the Elbe and all tributaries had lower biovolumes compared to the main stream (Fig. 3.4d). A comparison between Rhine and Elbe revealed strongly varying chlorophyll *a* concentrations and phytoplankton biovolumes in the Rhine during both sampling campaigns and generally higher chlorophyll concentrations and higher total phytoplankton biovolumes in the main tributaries (Fig. 3.3a,b; Fig. 3.4a,b). By contrast, during both sampling campaigns in the Elbe, chlorophyll *a* concentrations increased to more than 100 µg L^{-1} and the main tributaries had low chlorophyll concentrations in comparison to the main stream (Fig. 3.3c,d) which matches the lower phytoplankton biovolumes in almost all tributaries (Fig. 3.4c,d).

In the Rhine, phytoplankton net rates of increase between two sampling sites were 0.06 d^{-1} (doubling time of 10.6 days) in 2010 and 0.60 d^{-1} (doubling time of 1.2 days) in 2011. In the Elbe, net rates of increase were 0.39 d^{-1} (doubling time of 1.8 days) in 2009 and 0.14 d^{-1} (doubling time of 4.9 days) in 2011.

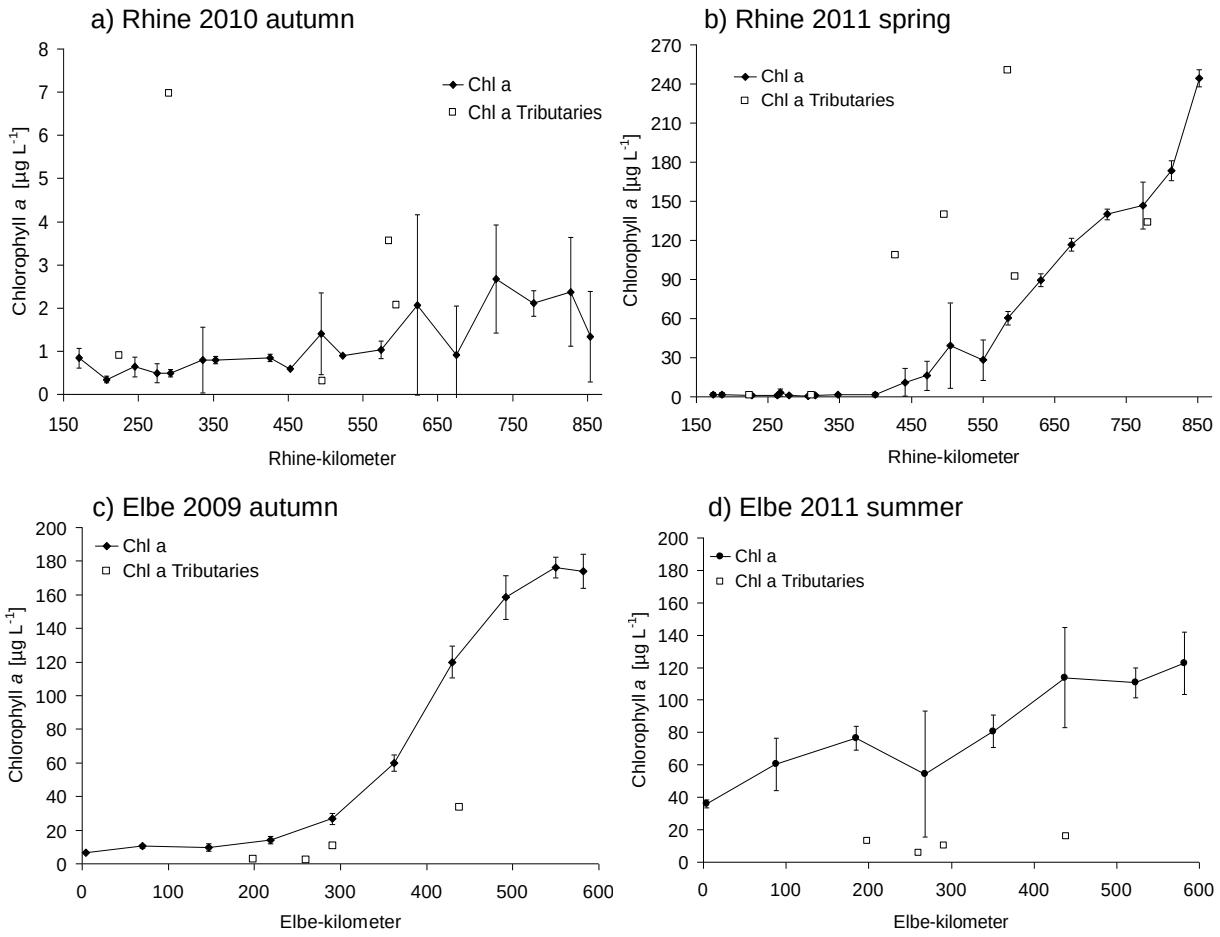

Fig. 3.3: Chlorophyll *a* development during downstream transport in the Rhine in autumn 2010 (a) and spring 2011 (b) and in the Elbe in autumn 2009 (c) and summer 2011 (d). Dots present values of the main river as a mean of the samples collected from the left side, the right side, and the middle of the river, ± standard deviation. Empty symbols present values of main tributaries or backwaters (a: Rest-Rhine km 225, Rest-Rhine km 291, Main, Lahn, Moselle; b: Rest-Rhine km 225, Ill, Neckar, Main, Lahn, Moselle, Ruhr, c and d: Schwarze Elster, Mulde, Saale, Havel).

The phytoplankton load of the rivers was calculated in order to estimate the influence of the tributaries on the phytoplankton in the main stream (Table 3.3). In September 2010, the Rhine was inoculated with a high phytoplankton biomass from the river Moselle, with a contribution of 24 % to the total chlorophyll load of the main river. In May 2011, the tributaries Neckar and Main provided an extraordinarily high input of chlorophyll *a*. The chlorophyll load of the Neckar was 5.6 and the load of the Main was 1.4 times higher compared to the Rhine. By contrast, the tributaries of the Elbe were diluting the concentration of the main stream, as they

had only low chlorophyll *a* loads and contributed at most 8.5 % to the load of the main stream.

Table 3.3: Chlorophyll *a* loads of the Rhine, the Elbe and their major tributaries.

Chlorophyll load Rhine 2010	Discharge ($m^3 s^{-1}$)	Tributary	Load Rhine before tributary (kg s^{-1})	Load of tributary (kg s^{-1})	% load of the main river
Speyer (km 400)	942	Neckar	7.91×10^{-4}	-	-
Worms (km 443)	1030	Main	1.45×10^{-3}	4.44×10^{-5}	3.07
Kaub (km 546)	1270	Lahn	1.31×10^{-3}	8.17×10^{-5}	6.21
Koblenz (km 591)	1275	Moselle	1.32×10^{-3}	3.13×10^{-4}	23.69
Chlorophyll load Rhine 2011	Discharge ($m^3 s^{-1}$)	Tributary	Load Rhine before tributary (kg s^{-1})	Load of tributary (kg s^{-1})	% load of the main river
Speyer (km 400)	672	Neckar	1.19×10^{-3}	6.61×10^{-3}	555.62
Worms (km 443)	716	Main	7.16×10^{-2}	1.65×10^{-2}	142.30
Kaub (km 546)	882	Lahn	2.49×10^{-2}	3.01×10^{-3}	12.07
Koblenz (km 591)	898	Moselle	5.41×10^{-2}	4.16×10^{-3}	7.68
Chlorophyll load Elbe 2009	Discharge ($m^3 s^{-1}$)	Tributary	Load Elbe before tributary (kg s^{-1})	Load of tributary (kg s^{-1})	% load of the main river
Torgau (km 154)	155	Schwarze Elster	1.48×10^{-3}	1.56×10^{-5}	1.05
Wittenberg (km 214)	168	Mulde	2.34×10^{-3}	5.06×10^{-5}	2.17
Aken (km 275)	195	Saale	5.21×10^{-3}	4.41×10^{-4}	8.46
Tangermünde (km 388)	240	Havel	1.44×10^{-2}	9.35×10^{-4}	6.51
Chlorophyll load Elbe 2011	Discharge ($m^3 s^{-1}$)	Tributary	Load Elbe before tributary (kg s^{-1})	Load of tributary (kg s^{-1})	% load of the main river
Torgau (km 154)	268	Schwarze Elster	9.92×10^{-3}	3.78×10^{-4}	3.81
Wittenberg (km 214)	311	Mulde	2.06×10^{-2}	3.60×10^{-4}	1.75
Aken (km 275)	394	Saale	2.15×10^{-2}	6.32×10^{-4}	2.94
Tangermünde (km 388)	467	Havel	3.77×10^{-2}	2.93×10^{-3}	7.76

Phytoplankton composition

In September 2010, the phytoplankton biovolume in the Rhine was permanently dominated by Baccillariophyceae (Fig. 3.5a,b). 54 % of the Bacillariophyceae were represented by *Cocconeis* sp. (25 %), *Melosira varians* (15 %) and *Fragilaria* sp. (14 %). The second most important phytoplankton class was the Cryptophyceae, followed by the Cyanophyceae, which increased in importance occasionally along the investigated river reach. The Cryptophyceae presented a high fraction of total phytoplankton biovolume in the Rest-Rhine (Rhine-km 291) and in the tributary Moselle in 2010. Within the Cyanophyceae, the colony forming species *Oscillatoria* sp. represented 83 %. The Rest-Rhine and the Lahn had very high phytoplankton biovolumes, twice as high as the main stream. In 2011, the total phytoplankton biovolume was 3 – 7 fold higher compared to 2010 in the free-flowing part of the river and diatoms mostly dominated the phytoplankton community. 58 % of the Bacillariophyceae were represented by *Fragilaria* sp. (30 %), *Melosira varians* (14 %) and *Stephanodiscus* sp. (14 %). Concerning the Cyanophyceae, the nitrogen-fixing species *Aphanizomenon gracile* was

dominant (71 %). As pointed out in the preceding section ‘Oxygen and phytoplankton development’, the tributaries of the free-flowing part had higher phytoplankton biovolumes compared to the main stream.

In the Elbe in autumn 2009, the phytoplankton biovolume was mainly constituted of diatoms (Fig. 3.5c,d). Downstream, the importance of Cyanophyceae increased and they presented the second most important phytoplankton class along the last hundred kilometers ahead of the Geesthacht Weir (Elbe-km 582). In the same river reach, the proportion of Chlorophyceae increased. In the tributary Havel, Cyanophyceae presented a high fraction of the total phytoplankton biovolume. The phytoplankton biovolume was in the same range in 2011, with a less pronounced increase downstream and a more uniform biovolume distribution among the algal classes. All tributaries, except the Havel in 2009, showed lower phytoplankton biovolumes compared to the preceding value of the main stream. This stands in contrast to the Rhine and confirms the observation of comparatively lower chlorophyll *a* values in the tributaries of the Elbe and higher chlorophyll values in the tributaries of the Rhine (cf. section ‘Oxygen and phytoplankton development’).

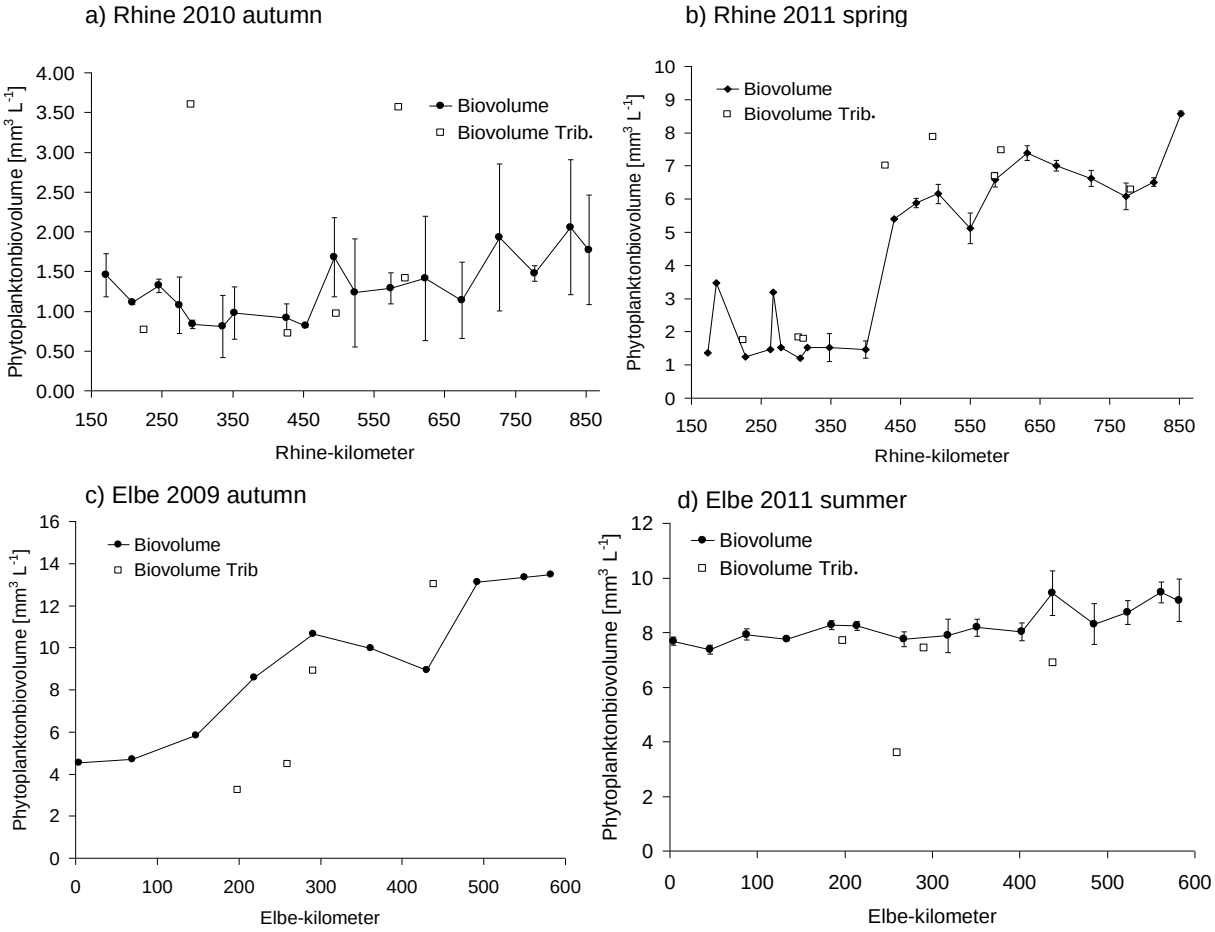

Fig. 3.4: Phytoplankton biovolume during downstream transport in the Rhine in autumn 2010 (a) and spring 2011 (b) and in the Elbe in autumn 2009 (c) and summer 2011 (d). Dots present values of the main river as a mean of the samples collected from the left side, the right side, and the middle of the river, ± standard deviation. Only in autumn 2009 (c) dots present values of the main river as a mean of the samples collected from the middle of the river twice a day at one sampling station. Empty symbols present values of main tributaries or backwaters (a: Rest-Rhine km 225, Rest-Rhine km 291, Neckar, Main, Lahn, Moselle; b: Rest-Rhine km 225, Kinzig, Ill, Neckar, Main, Lahn, Moselle, Ruhr; c and d: Schwarze Elster, Mulde, Saale, Havel).

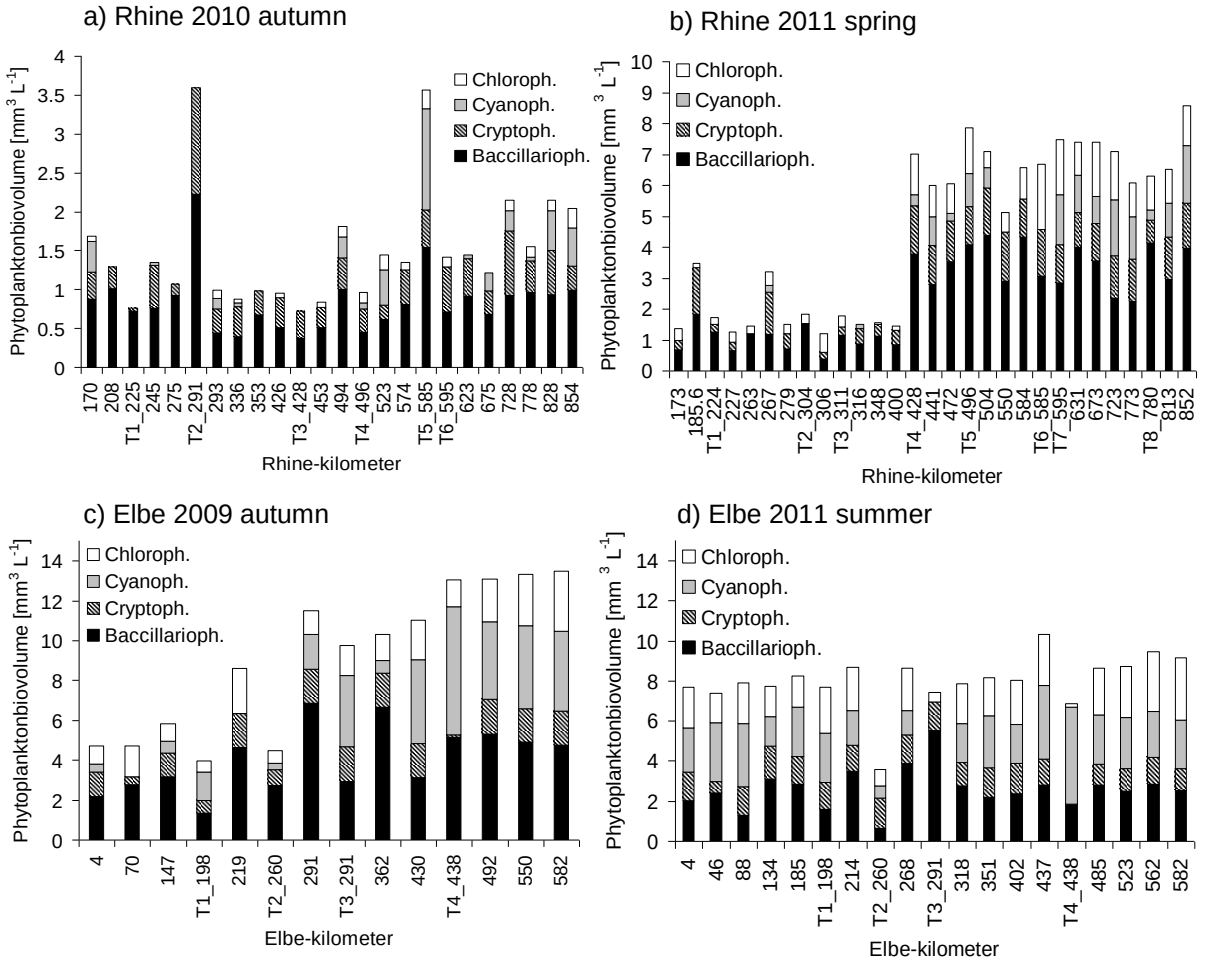

Fig. 3.5: Biovolume of phytoplankton classes (Baccillariophyceae, Cryptophyceae, Cyanophyceae, and Chlorophyceae) during downstream transport in the Rhine in autumn 2010 (a) and spring 2011 (b) and in the Elbe in autumn 2009 (c) and summer 2011 (d). Presented are values of the main river as a mean of the samples collected from the left side, the right side and the middle of the river. Only in autumn 2009 (c) values of the main river, as a mean of the samples collected from the middle of the river twice a day at one sampling station, are presented. Tributaries or backwaters are designated T1-T8 (a: Rest-Rhine km 225, Rest-Rhine km 291, Neckar, Main, Lahn, Moselle; b: Rest-Rhine km 225, Kinzig, Ill, Neckar, Main, Lahn, Moselle, Ruhr; c and d: Schwarze Elster, Mulde, Saale, Havel).

Zooplankton development

In May 2010, the zooplankton abundance in the Rhine at the beginning (Rhine-km 170) and at the end (Rhine-km 854) of the Lagrangian sampling campaign stayed similarly low: 4 and 3 ind. L^{-1}, reaching maximal values of 18 ind. L^{-1} in between (Fig. 3.6a,b). In the Rest-Rhine at Rhine-km 291, a comparatively high zooplankton abundance of 178 ind. L^{-1} prevailed. Compared to the main river, the Lahn had a higher zooplankton abundance with 15 ind. L^{-1}. In

spring 2011, zooplankton abundance increased from 7 ind. L^{-1} at Rhine-km 400 to 358 ind. L^{-1} at the end of the free-flowing part (Rhine-km 773). During downstream passage, a maximal zooplankton abundance in the free-flowing part of up to 435 ind L^{-1} was present (Rhine-km 504) downstream the confluence of the Main. In the tributary Neckar, zooplankton abundance even reached 4,728 ind. L^{-1}, and in the Lahn and the Ruhr zooplankton abundances were approximately 3,000 ind. L^{-1}.

Zooplankton abundance was lower in the Elbe and in September 2009, a 15-fold increase from 7 ind. L^{-1} at Elbe-km 4 to 108 ind. L^{-1} at Elbe-km 582 could be detected (Fig. 3.6c,d). From all tributaries, the Havel presented the highest abundance of 117 ind. L^{-1}. Like the weak phytoplankton increase, in 2011, zooplankton abundance increased only slightly downstream (from 11 to 44 ind. L^{-1}), and in the tributaries zooplankton abundances were lower or in the range of the concentrations of the main stream (maximum in the Mulde and the Havel: 29 ind. L^{-1}).

The Mollusca represented the most important zooplankton phylum in terms of abundance in the Rhine in September 2010, with increasing abundances downstream (Fig. 3.7a,b). The Mollusca were composed of Dreissena veliger larvae (83 %), Gastropoda indet. (16 %) Lamellibrancha indet. veliger larvae (0.4 %). The Rest-Rhine, the Neckar and the Moselle were characterized by higher zooplankton biovolumes compared to the preceding value in the main stream, and the tributaries Lahn and Moselle revealed high proportions of bivalve larvae. In 2011, congruent to the phytoplankton biovolume development, zooplankton abundance increased dramatically in the free-flowing part of the river. The Neckar, the Main, the Lahn, the Moselle and the Ruhr increased zooplankton biovolumes of the main stream, as they all presented higher zooplankton biovolumes, predominantly composed of rotifers. As in 2010, there was a prominent dominance of bivalve larvae in the main river.

In terms of zooplankton biomass in autumn 2009 in the Elbe, Crustacea represented by far the most important class with a pronounced increase downstream, followed by Rotifera with a less strong increase (Fig. 3.7c,d). 75 % of the Crustacea were composed of Copepoda larvae, Ostracoda and Daphnia. Zooplankton biovolumes in the tributaries were in the range of those in the main river, with the exception of the Havel showing higher zooplankton values. In summer 2011, the importance of Crustacea increased downstream, while Mollusca dominated at the beginning and at the end of the investigated river reach. Tributary biovolume concentrations were again in the range of the main stream.

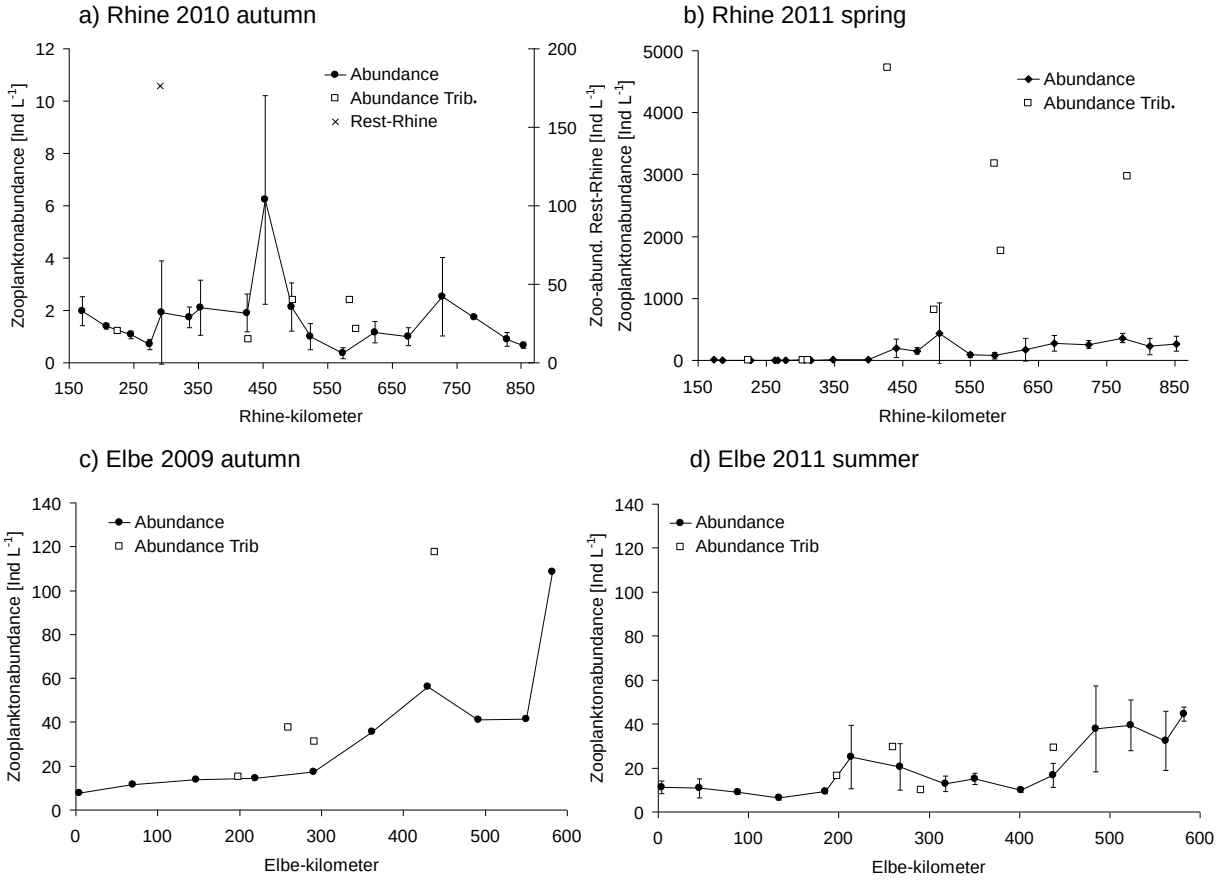

Fig. 3.6: Zooplankton abundance during downstream transport in the Rhine in autumn 2010 (a) and spring 2011 (b) and the Elbe in autumn 2009 (c) and summer 2011 (d). Dots present values of the main river as a mean of the samples collected from the left side, the right side, and the middle of the river, ± standard deviation. Only in autumn 2009 (c) values of the main river as a mean of the samples collected from the middle of the river twice a day at one sampling station are presented. Empty symbols present values of main tributaries or backwaters (a: Rest-Rhine km 225, Rest-Rhine km 291, Neckar, Main, Lahn, Moselle; b: Rest-Rhine km 225, Kinzig, Ill, Neckar, Main, Lahn, Moselle, Ruhr; c and d: Schwarze Elster, Mulde, Saale, Havel).

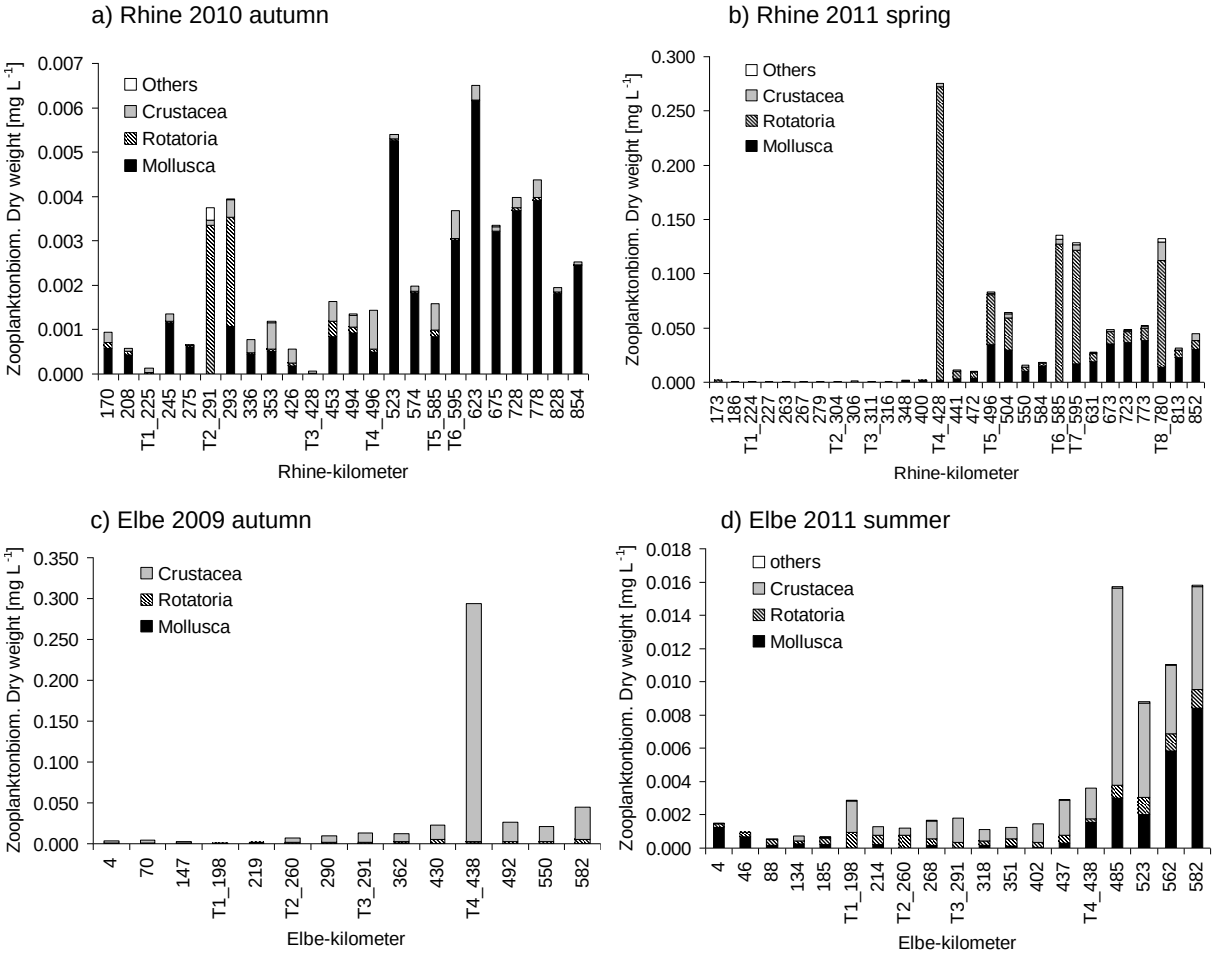

Fig. 3.7: Biomass of zooplankton classes (Mollusca, Rotifera, and Crustacea) during downstream transport in the Rhine in autumn 2010 (a) and spring 2011 (b) and in the Elbe in autumn 2009 (c) and summer 2011 (d). Presented are values of the main river as a mean of the samples collected from the left side, the right side, and the middle of the river. Only in autumn 2009 (c) values of the main river as a mean of the samples collected from the middle of the river twice a day at one sampling station are presented. Tributaries or backwaters are designated T1-T8 (a: Rest-Rhine km 225, Rest-Rhine km 291, Neckar, Main, Lahn, Moselle; b: Rest-Rhine km 225, Kinzig, Ill, Neckar, Main, Lahn, Moselle, Ruhr; c and d: Schwarze Elster, Mulde, Saale, Havel).

Bivalve development

The clam *Corbicula* sp. (*Corbicula fluminea* and *Corbicula fluminalis*) inhabited the sediments of the Rhine in numbers up to 1,248 ind. m^{-2} (survey of April and May 2011), while it could only be detected occasionally during a sampling campaign performed in June 2011 in the Elbe where a maximal abundance of 64 ind. m^{-2} was reached (Fig. 3.8). In the same year,

the sessile mussel *Dreissena* sp. (*Dreissena polymorpha* and *Dreissena rostriformis*) reached maximum abundances of 5,528 ind. m^{-2} in the Rhine, and up to 3,184 ind. m^{-2} in the Elbe, where abundances were mostly below 500 ind. m^{-2}. In the Rhine, highest bivalve abundances could be found between Rhine-km 300 to 450.

The shell length of *Corbicula* sp. showed a distribution across a wide size range between 11 to 29 mm in the Rhine (survey May 2010, Fig. 3.9). At the end of the investigated river reach bivalve shell length distribution shifted towards longer bivalve shell lengths. The same could be observed for *Dreissena* sp., the frequency of larger mussels increased downstream. In 2010, maximal abundances of *Corbicula* sp. were 1,472 ind. m^{-2} and *Dreissena* sp. reached maximal abundances of 3,112 ind. m^{-2}.

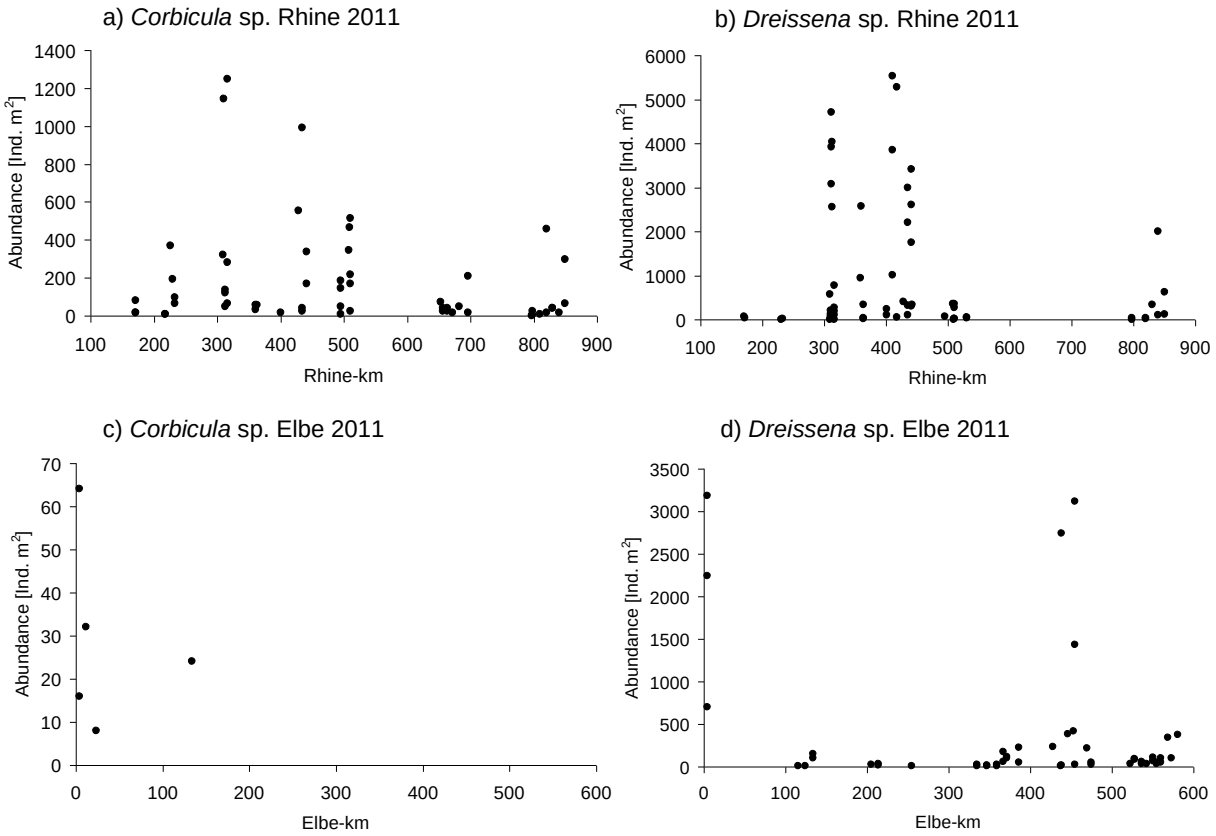

Fig. 3.8: Abundance of *Corbicula* sp. and *Dreissena* sp. in April/May 2011 in the Rhine and in June 2011 in the Elbe.

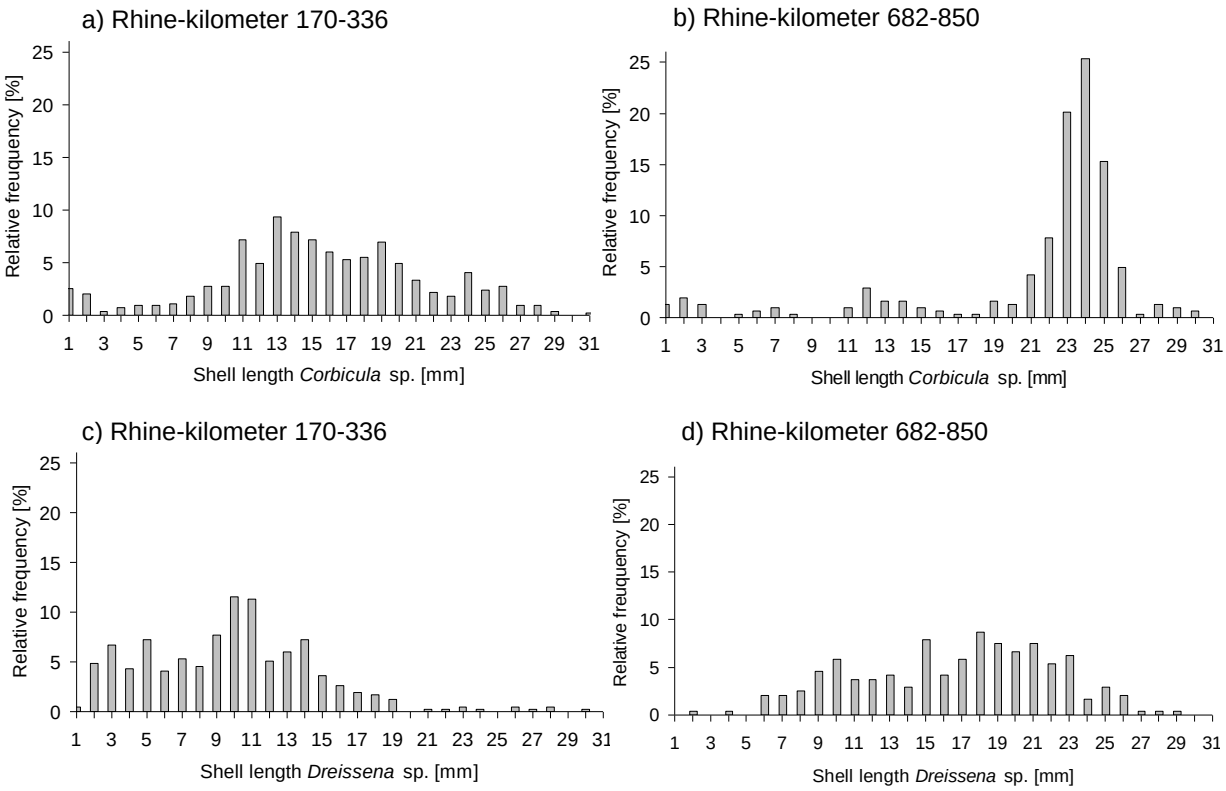

Fig. 3.9: Frequency distributions of bivalve shell length (*Corbicula* sp. and *Dreissena* sp.) in May 2010 in the Upper Rhine (left) and the Lower Rhine (right).

3.5 Discussion

The present study demonstrates a high longitudinal variability in chlorophyll *a* development in both rivers, the Rhine and the Elbe, as a result of the conditions prevailing during downstream transport in the free-flowing part, irrespective of start values in the upper river reaches. An exceptional event demonstrated that obviously a strong phytoplankton production during favorable low flow conditions can lead to a pronounced regime shift and to unusually high chlorophyll concentrations in the Rhine. Tributaries can impose different and river system specific alterations in plankton abundances of the main stream, while within-river processes still seemed to govern plankton dynamics.

Longitudinal phytoplankton development and biovolume composition

High temporal and longitudinal dynamics in phytoplankton biomass prevail in the Rhine. In September 2010, chlorophyll *a* values remained below 5 µg L^{-1} during the entire river length and phytoplankton biovolume was low, whereas in May 2011 there was an extreme event with a high total phytoplankton biomass and unusually high chlorophyll *a* values (244 µg L^{-1} at Rhine-km 854). The start values at the beginning of the free-flowing part were below 2 µg L^{-1} in both years, but despite these low chlorophyll concentrations in the upper reaches, very high chlorophyll concentrations were measured in the lower reaches in 2011. The tributaries contributed significantly to the chlorophyll *a* concentration in the main stream and therefore were an important source of phytoplankton. Low chlorophyll *a* concentrations like in September 2010 are common for the Rhine. Average chlorophyll concentrations decreased significantly over the last two decades (Friedrich and Pohlmann 2009; cf. Chapter 2). Some of this decrease was attributed to the invasion of benthic filter feeders (Akopian et al. 2001). In this context, the 100-fold increase in chlorophyll concentrations along the river found in May 2011 is surprising, because the chlorophyll concentrations measured during the survey considerably exceeded all values measured during the last three decades. At Bimmen (Rhine-km 865), the chlorophyll *a* peaks were below 180 µg L^{-1} from 1979 to 1997 and from 1998 to 2004, maximal chlorophyll concentrations lay in the range of 37 to 83 µg L^{-1} (Friedrich and Pohlmann 2009). In contrast to the steadily increasing chlorophyll values in 2011, there was an abrupt increase in total phytoplankton biovolume at Rhine-km 400 to 450 which could be a result of the transition from the deep, impounded river reach to the shallower free-flowing river reach starting at Rhine-km 336. The phytoplankton community was dominated by diatoms and the second dominant group were the Cryptophyceae. A dominance of diatoms is typical for large, turbulent and nutrient enriched rivers (Gosselain et al. 1994; Reynolds and Descy 1996). Likewise, De Ruyter van Steveninck et al. (1990) reported consistently dominant diatoms in the lower Rhine. In 2010, smaller species, like *Cocconeis* sp., were numerous while larger colony forming species, like *Fragilaria* sp., accounted for the largest fraction of the diatoms in 2011. Hence, the abrupt increase in phytoplankton biovolume in 2011 might result from a dominance of colony forming species. The extremely low flow conditions obviously presented favorable growth conditions especially for colony forming species, which are probably less affected by grazing due to their size and hence less prone to loss processes by benthic filter feeders (cf. section ‘Controlling

factors and the role of bivalves'). Moreover, it was observed that phytoplankton colonies can be composed of more cells during favorable growth conditions, hence the size of a single colony can increase (Wagner 1998).

Chlorophyll *a* concentrations in the Elbe increased longitudinally during both surveys. Maximal chlorophyll *a* values of 180 µg L^{-1} in 2009 and 120 µg L^{-1} in 2011 could be observed in the lower reaches of the Elbe (Elbe-km 560), which represented a 4- and 27-fold increase compared to the start values (Elbe-km 4). In the upper reaches, chlorophyll values were lower in 2009 (6.5 µg L^{-1}) compared to 2011 (36 µg L^{-1}), hence phytoplankton net increases in the free-flowing part of the Elbe can lead to high chlorophyll concentrations in the lower reaches irrespective of the start values. Chlorophyll values in the order of 200 µg L^{-1} were frequently observed at the end of the free-flowing part of the Elbe (Guhr et al. 2004). Like in the Rhine, diatoms were dominating phytoplankton biovolume in the Elbe, followed by Chlorophyceae. Usually in large rivers, Chlorophyceae are present in high abundances next to the diatoms, because they have characteristically small celled colonies and can cope with high flow velocities. No abrupt increase in phytoplankton biovolume along the Elbe could be detected and biovolume increase was less strong, compared to the pronounced chlorophyll increase in September 2009. Possibly, a higher chlorophyll content per cell was present in the lower, light-limited reaches of the river.

It was shown that in both rivers, high chlorophyll concentrations in the middle and lower river reaches were a result of high within-river net phytoplankton increases in the free-flowing part rather than a result of the start values in the upper reaches. It could be confirmed that higher chlorophyll concentrations in the lower reaches of the Elbe compared to the Rhine did not result mainly from higher import of dam-influenced upper reaches (hypothesis i). In autumn 2010, lower chlorophyll concentrations prevailed in the lower reaches of the Rhine in comparison to the Elbe, confirming hypothesis i. By contrast during the extreme event in spring 2011, other mechanisms prevailed in the Rhine (cf. section 'Controlling factors and the role of bivalves').

Contrasting influence of tributaries on phytoplankton composition and chlorophyll load

In the Rhine, Cryptophyceae were contributed from the impounded tributaries in 2010. Cryptophyceae are commonly favored in areas of lower water flow velocities, conditions

prevailing in the downstream part or in impounded rivers (Bahnwart et al. 1998). The Havel influenced the phytoplankton community in the downstream section of the Elbe by the input of Cyanophyceae. All major tributaries of the Rhine had higher chlorophyll *a* concentrations than the main stream and thereby presented a supply to the concentration in the main stream. In May 2011, the total phytoplankton biovolume was extremely high in the tributaries leading into the free-flowing part of the river and probably contributed to the abrupt increase in total phytoplankton biovolume. Different investigations of plankton development in the Rhine confirm the observation in the present study that the contribution of phytoplankton from tributaries is rather important (Tubbing 1994; Scherwass et al. 2010). In contrast to the Rhine, tributaries of the Elbe had mostly lower chlorophyll *a* concentrations and phytoplankton biovolumes compared to the main stream. This means that the Elbe provides favorable conditions for phytoplankton that grows here independently of lateral inputs. Whereas in the present study the contribution of chlorophyll *a* loads to the main river load remained below 10 % in the Elbe, much higher inputs of up to 555 % were observed in the Rhine. During the vegetation period, 66 – 85 % of the chlorophyll *a* was produced in the Elbe (Guhr et al. 2004), whereas in the Rhine, inputs from tributaries accounted for approx. 50 % of the chlorophyll *a* load (ICPR 1997). Longitudinal growth of phytoplankton along the Elbe was observed in several studies, where increases by factors between 3 and 6 have been found and maximum chlorophyll values of 190 and 220 µg L^{-1} (Böhme et al. 2002; Guhr et al. 2004; Pusch et al. 2009). Guhr et al. (2004) stated a decrease in chlorophyll *a* levels near the Geesthacht Weir (Elbe-km 560) which is in accord with the decreasing oxygen concentrations observed ahead of the Geesthacht Weir in both surveys of the present study.

It was revealed that in both rivers, tributaries had contrasting impacts on the phytoplankton development. Hence, tributaries had the potential to supply phytoplankton concentrations in the Rhine and to dilute concentrations in the Elbe (hypothesis ii). Nevertheless, river-internal processes still seemed to dominate these tributary impacts.

Phytoplankton net increase between two sampling sites

The calculated net increases, standing for rates of biomass change along the river, were 0.60 d^{-1} during the extreme event in spring in the Rhine (2011) and 0.14 d^{-1} during summer in the Elbe (2011). In September, net rates of increase were 0.06 d^{-1} in the Rhine (2010) and 0.39 d^{-1} in the Elbe (2009). This was in the range of the growth rate determined by Köhler et al.

(2002) for the rivers Spree and Warnow, who found growth rates of 0.12 – 0.79 d^{-1} in summer and - 0.25 to 0.89 d^{-1} in May and April. In addition to these growth rates measured in bottle experiments by excluding benthic filter feeders, they also determined the rate of biomass change along the rivers and found negative values, indicating high losses by grazing and sedimentation in the field. In the present study, the contrasting net rates of increase during autumn in both rivers was accompanied by high phytoplankton concentrations measured in the Elbe (2009) and low concentrations measured in the Rhine (2010) (cf. section 'Longitudinal phytoplankton development and biovolume composition'). Hence, compared to the Rhine, higher net phytoplankton increases along the free-flowing part of the river prevailed in the Elbe, resulting in high chlorophyll values in the lower reaches (hypothesis i). Lower net increases were found in the free-flowing part of the Rhine accompanied by low chlorophyll values in the lower reaches. Obviously, strong loss processes prevailed in the Rhine, leading to low net rates of increase in phytoplankton biomass (see section 'Controlling factors and the role of bivalves'). During the exceptional extreme event in the Rhine in 2011, obviously other mechanisms prevailed (see 'Controlling factors and the role of bivalves').

Zooplankton development and composition

Zooplankton usually develops in the lower potamal or in impounded sections of rivers, where water retention time is high enough to allow the reproduction of these organisms. Riverine zooplankton communities are commonly dominated by rotifers, rather than crustaceans, because they have shorter generation times and the ability of parthenogenetic reproduction (Viroux 2002; Lair 2006). Extremely low plankton abundances, prevailing in the upper part of the Rhine, are a result of low plankton loads from pre-alpine lakes, and the hydro-morphological conditions in this deep, canalized river reach (Bergfeld et al. 2011). Even in the lower section of the Rhine, zooplankton biomass is usually low (De Ruyter van Steveninck et al. 1992; ICPR 1997; Weitere et al. 2005). This has been attributed to relatively short travel times, adverse effects of turbulence as well as to low food concentrations and high grazing pressure from benthic filter feeders (Ietswaart et al. 1999; Schöl et al. 2002; Sluss et al. 2008). The results of the present study from September 2010 in the Rhine agree with these general observations and only a weak zooplankton increase downstream was observed. By contrast in Mai 2011, total zooplankton abundances were higher (77 ind. L^{-1} at Koblenz) and strongly increased downstream which showed the potential for zooplankton growth under

optimized conditions. Still, rotifer abundances which alone accounted for 190 ind. L^{-1} at the measuring station Koblenz in the year 2000 reported by Bergfeld et al. (2009), could not be found in the present study. Maximal total zooplankton abundances of 358 ind. L^{-1} at Rhine-km 773 were only moderately high compared to reported maximal abundances of 1,000 ind. L^{-1} for rotifers alone in the Seine (Billen et al. 1994) and 4,000 ind. L^{-1} for rotifers alone in the Meuse (Gosselain et al. 1994). During Lagrangian sampling campaigns in 1990 in the Rhine, rotifer abundances were 1,728 ind. L^{-1} (De Ruyter van Steveninck 1992). Rotifers and mussel larvae (veliger larvae of *Dreissena* sp.) were found to dominate community composition of zooplankton in the Rhine (De Ruyter van Steveninck et al. 1992; Friedrich and Pohlmann 2009) which is in accordance with the results of the present study for 2011. The importance of protozooplankton in the Rhine, as highlighted in diverse studies (Weitere et al. 2005; Bergfeld et al. 2009) could not be verified in the present study, because proto-zooplankton was not determined. The results of the present study only partly confirm the general finding that in the Rhine, abundance and biovolume of plankton components is generally low (ICPR 2002; Scherwass and Arndt 2005; Weitere et al. 2005; Bergfeld et al. 2009) and underline the importance of the prevailing longitudinal processes which can lead to exceptional events of high plankton growth. Thus for the Rhine, congruent to the finding of Junk et al. (1989), it can be concluded that irrespective of the start values, the potential of planktonic organisms to increase in abundance depends on prevailing conditions during downstream transport.

In contrast to the Rhine, high zooplankton abundances of more than 10,000 ind. L^{-1} are occasionally observed during late summer in the lower sections of the Elbe (Karrasch et al. 2001; Holst et al. 2002). This could not be confirmed in the present study with maximal total zooplankton abundances of only 44 ind. L^{-1} and 108 ind L^{-1} at Elbe-km 582 which is rather low compared to reported maximal rotifer abundances of 5,800 ind. L^{-1} in the river Loire during low flow conditions in 1995 (Lair et al. 1997).

Impact of tributaries on zooplankton

During the extreme event in the Rhine in 2011, tributaries were mainly characterized by very high zooplankton abundances (around 3,000 – 4,700 ind. L^{-1}) compared to the main river (around 400 ind. L^{-1}), presenting an additional input of planktonic organisms. In total, zooplankton abundance increased 50-fold during downstream transport, which was enhanced

by the high abundances in the tributaries. By contrast, zooplankton abundances in the tributaries were lower in the Elbe and predominantly in the range of the main river, except for the Havel. These low zooplankton abundances in the Elbe tributaries agree with the work of Meister (1994). Concerning the zooplankton composition, the tributaries of the Rhine frequently carried mussel larvae (veliger larvae of *Dreissena* sp.), while in the tributaries of the Elbe, mussel larvae could rarely be found. During a Lagrangian sampling campaign performed in 2000, the Moselle exceeded the metazooplankton load of the Rhine by 57 % (Scherwass et al. 2010). This corresponds to the results of the present study and the observation that the contribution of zooplankton from tributaries is rather important.

Hence, the second hypothesis (hypothesis ii), that tributaries can potentially alter the longitudinal plankton developments in the Rhine and the Elbe could be confirmed for zooplankton. Tributaries had contrasting impacts on phyto- and zooplankton biomass, they were diluting plankton concentrations in the Elbe, while they were supplying concentrations in the Rhine (cf. section 'Contrasting influence of tributaries on phytoplankton composition and chlorophyll load'). Tributaries are therefore one possible control mechanism influencing plankton communities of the main stream.

Controlling factors

High plankton concentrations, so-called phytoplankton spring blooms or peaks, occur typically in spring because during this time of the year, high winter flood events recede and favorable discharge conditions often coincide with high light intensities (cf. Chapter 2). Discharge conditions play an important role for phytoplankton growth, as they determine the travel time of the water and are associated with light conditions in the water column. The high chlorophyll concentrations in the Rhine in 2011 were accompanied by extremely low discharge with mean travel times of the water of 10 days along the sampled river section. By contrast, discharge was higher and travel time shorter (8 days) in 2010 when lower chlorophyll *a* values were measured. Besides longer travel times, low discharge conditions also ameliorate the light climate in the water column, whereas high discharge conditions with deeper and often more turbid water may inhibit phytoplankton growth by light limitation. Thus, the spatio-temporal development of hydraulic conditions has a strong impact on the longitudinal phytoplankton development, irrespective of start chlorophyll values. Ietswaart et al. (1999) who performed two longitudinal surveys in spring and summer of 1995 confirmed

the occurrence of very low chlorophyll *a* values, and explained this by the high discharge conditions prevailing in 1995 leading to shorter water flow times. The opposing mechanism of low discharge conditions was supposed to cause high chlorophyll concentrations in 1990 observed by Admiraal et al. (1994). On the one hand, low discharge conditions can promote phytoplankton growth due to prolonged residence times and improved light conditions, and on the other hand low flows can enhance grazing impacts on phytoplankton due to a stronger bentho-pelagic coupling (cf. section 'Controlling factors and the role of bivalves').

Light is generally considered to limit phytoplankton growth in rivers (Basu and Pick 1996). During the surveys of the present study in the Rhine, light penetration at the bottom was mostly above 1 % of surface light irradiance, while in the Elbe, water depth was mostly equal to the compensation depth. This means that positive plankton growth was possible, and neither in the Rhine nor in the Elbe strict light limitation prevailed. However, a downstream decrease of mean irradiance in the water column occurred, as reported earlier for both rivers (Ietswaart et al. 1999; Guhr et al. 2004). As water temperature did not reach any extremes during the surveys of the present study, the influence on phytoplankton growth was assumed to be of little account.

Nutrient concentrations decreased downstream in 3 out of the 4 sampling campaigns of the present study. Algal growth limiting concentrations were reached in the most downstream part in September 2009 in the Elbe (orthoP = 0.01 mg L^{-1}) and in May 2011 in the Rhine (orthoP < 0.01 mg L^{-1}) which could be explained by the strong phytoplankton growth. Growth limiting concentrations are approximately in the range of 0.02 mg L^{-1} for orthoP and nitrate but the limiting macronutrient is determined by the ratio between N:P (Lampert and Sommer 1999). The increasing seston values observed in all sampling campaigns may be enhanced by an additional input of particulate substances by tributaries and by the growth of phytoplankton. All main tributaries had higher levels of seston compared to the Rhine. The observed phenomenon of decreasing concentrations of dissolved nutrients and increasing seston and chlorophyll *a* concentrations is typical for eutrophic rivers (Lair and Reyes-Marchant 1997; Guhr et al. 2004; Twiss et al. 2010). It can be attributed to sufficiently long water residence times allowing algae to take up nutrients and grow. Only in situations with low phytoplankton growth, like in the Rhine in September 2010, increasing nutrient concentrations were detected, as reported earlier (Ietswaart et al. 1999).

Controlling factors and the role of bivalves

Apart from the hydrological, climatologic and chemical factors, the biological impact on phytoplankton should be taken into account. The results of the present study indicated high abundances of the invasive bivalves *Corbicula* sp. and *Dreissena* sp. in the Rhine in contrast to lower abundances in the Elbe. The maximal abundance of *Corbicula* sp. in the Rhine was 20 times higher compared to the Elbe, where *Corbicula* sp. was mostly absent. Likewise in the Rhine, *Dreissena* sp. frequently reached maximal abundances twice as high as in the Elbe where high abundances were exceptions. Hence, the grazing potential of bivalves on the planktonic compartment was much higher in the Rhine. Bivalve presence was evenly distributed in the Rhine with highest abundances and high grazing potentials on river plankton between Rhine-km 300 to 450, which is the warmest part of the river due to heated discharges by industrial facilities. The results of the water quality modeling approach confirmed that river water temperatures were highest between Rhine-km 300 to 450 (cf. Chapter 4). In the lower section of the river, with moderate bivalve abundances, the frequency of larger shell length increased, probably also leading to an enhanced grazing potential on planktonic organisms. Despite the presence of suitable sandy substrates, *Corbicula* sp. could only be detected within the first 140 kilometers sampled in the Elbe, whereas the sessile bivalve *Dreissena* sp. was evenly distributed with maximal abundances at the beginning and at the end of the river reach investigated. Hard substrates like rocks are required for the bysally-attached mussels, hence the groins present a suitable habitat for *Dreissena* sp. (Mellina and Rasmussen 1994). Today, *Corbicula fluminea* is the most common bivalve in several rivers of the northern hemisphere, including the Rhine (Karatayev et al. 2005). Benthic filter feeders with the potential to reduce phytoplankton biomass were observed in many rivers, for instance in the Danube (Reckendorfer et al. 2006), the Moselle (Schöl et al. 1999), the Severn (Köhler 1997), and in the Rhine (Ietswaart et al. 1999; Schmidlin and Baur 2007). By contrast, abundances of bivalves are generally low in the Elbe and can therefore not control phytoplankton biomass. For the Rhine, the occurrence of high abundances of benthic filter feeding bivalves was often claimed to reduce chlorophyll contents (Viergutz et al. 2007; Weitere et al. 2009), especially at low discharge conditions (Ietswaart 1999; Weitere and Arndt 2002). Thus, the impact of benthic filter-feeders on the biomass of river plankton is maximal in summer when low discharge conditions are frequently encountered (Descy et al. 2003). Nevertheless, information about densities and biomass of bivalves in the Rhine is

rather scarce so that total in situ filtration rates are difficult to determine (Ietswaart et al. 1999; Schöll 2000; Imo et al. 2010).

In order to provide a rough estimation of the potential grazing impact of bivalves (*Dreissena* sp. and *Corbicula* sp.) in the Rhine, a scenario calculation might help. From the measurements of bivalve abundances in 2011, a mean bivalve density of 634 ind. m^{-2} can be derived. Assuming that one bivalve individual can filter about 100 ml ind^{-1} h^{-1} (Vohmann et al. 2009), 63.4 L m^{-2} h^{-1} could be filtrated. Per day 0.0634 m^3 m^{-2} h^{-1} could be filtrated which equals to a water column of 1.52 m day^{-1}. The Rhine has a mean water depth of 3 m and under these assumptions and depending on the particle concentration, bivalves could filter the entire water column within two days. Assuming a mean phytoplankton doubling time of one duplication per day, bivalves have the potential to regulate phytoplankton production. Depending on the water temperature, the particle concentration and the shell length, one bivalve can filter even more than 100 ml h^{-1}. Hence, lower net plankton increases in the Rhine observed in 2010 can potentially be explained by high densities of benthic filter feeders confirming the third hypothesis (hypothesis iii).

At extremely low discharge conditions in May 2011 in the Rhine, chlorophyll *a* values were unusually high (cf. section 'Longitudinal phytoplankton development and biovolume composition'), although water temperatures were high enough to support temperature sensitive filtration activity of bivalves (Sprung and Rose 1988; Lei et al. 1996; Weitere and Arndt 2002). A possible explanation could be that due to the extremely low discharge condition in May 2011, a large area of the lateral structures of the river bed with high abundances of bivalves fell dry, leaving behind a smaller ratio of water volume to river bottom inhabited by bivalves. This was not obvious from the measurements of bivalve abundances in 2011 which were as high as in 2010. But despite the high bivalve abundances in the remaining sediment covered by water, probably the total available habitat area was much smaller as most river banks fell dry.

The extreme event in the Rhine in 2011 demonstrates that under favorable growth conditions (favored by low discharge in combination with high light intensities) phytoplankton production (cf. section 'Longitudinal phytoplankton development and biovolume composition') could compensate potential phytoplankton loss processes. This means, that the positive effect of low flow conditions on phytoplankton production can compensate the potential negative effect of grazing by benthic filter feeding bivalves. Nevertheless, this was

an exceptional event and in recent years, phytoplankton amounts showed a decreasing trend in the Rhine where the loss processes seemed to dominate growth processes (cf. Chapter 2).

It can be summarized that higher chlorophyll values in the middle and lower reaches of the Elbe compared to the Rhine are a result of higher net phytoplankton increases along the free-flowing part rather than of different start values in the upper reaches (hypothesis i; cf. section 'Longitudinal phytoplankton development and biovolume composition' and 'Phytoplankton net increase between two sampling sites'). Plankton development in the longitudinal profile of a river is always prone to production and loss processes during downstream transport, and the prevailing plankton concentration is the result of these positive growth and negative loss processes. Despite contrasting impacts of tributaries, within-river processes still seemed to govern the characteristic plankton dynamics in the main stream (hypothesis ii; cf. sections 'Contrasting influence of tributaries on phytoplankton composition and chlorophyll load' and 'Impact of tributaries on zooplankton'). In 2010, low chlorophyll values were found in the Rhine which could be due to a high density of benthic filter feeders possibly exerting a strong grazing impact (hypothesis iii; see above 'Controlling factors and the role of bivalves'). On the other hand, the phytoplankton mass development observed in the Rhine in spring 2011 demonstrated that potential loss processes (e.g. due to a high grazing pressure on phytoplankton exerted by benthic filter feeders, which is generally reinforced during low flow conditions (cf. Weitere and Arndt 2002)) can obviously be outweighed by strong river-internal phytoplankton production rates. Despite similar chlorophyll concentrations in the upper reaches of the Rhine in 2010 and 2011, pronounced differences in the chlorophyll concentration in the downstream regions prevailed (cf. section 'Longitudinal phytoplankton development and biovolume composition'). Hence, extreme hydrological events can lead to an abrupt regime-shift changing the structure of the ecosystem with chlorophyll values considerably exceeding all values measured during the last three decades in the Rhine (244 µg L^{-1} at Rhine-km 854). This event stands in contrast to the decreasing trend in chlorophyll values observed during the time span 1990 – 2009 (cf. Chapter 2). Whereas during the beginning of the 1990s, higher phytoplankton amounts and higher chlorophyll concentrations were frequently found, the last decade was characterized by lower chlorophyll values. This may indicate an increasing impact of benthic filter-feeding bivalves.

4 Impacts of climate change on phytoplankton dynamics in the Rhine: a modeling approach

4.1 Abstract

To assess the impacts of climate change on river ecosystems is an essential task, because a good water quality should be preserved and the understanding of the links between climate and phytoplankton dynamics should be improved. Water quality simulation models help to investigate these possible effects and in the end help to consider mitigation options. The present study analyses climate change effects on the ecosystem of the river Rhine, the major navigable waterway for transportation in Germany. Therefore, a water quality model area of the free-flowing part of the Rhine was established and simulation calculations were performed based on different selected climate projections for the near (2021 – 2050) and for the far future (2071 – 2100). The model results indicated that the effects of climate change on phytoplankton biomass were rather small in the near and in the far future. The strongest chlorophyll increase could be detected at the end of the free-flowing part of the river at Rhine-km 860 in the far future (+ 4.22 µg L^{-1}). These increases in phytoplankton biomass might result from the discharge reduction of - 20 % which was the strongest discharge reduction found at Rhine-km 860 in the far future. More pronounced changes could be observed in the water temperature which increased in the far future by + 1.8°C at Rhine-km 460 and + 1.5°C at Rhine-km 860. The results revealed a decrease in oxygen concentrations in the far future by - 0.5 mg L^{-1} at Rhine-km 860 which was probably due to the lower solubility at higher water temperatures. It is possible that the rather small changes in phytoplankton biomass may result from the choice of the intermediate CO_2 emission scenario A1B (IPCC 2007). A more extreme emission scenario with more pronounced changes in climatologic conditions, like lower precipitation and lower flow conditions might provoke stronger responses of phytoplankton.

4.2 Introduction

Phytoplankton is the most important primary producer in large rivers and ecosystem properties, including oxygen concentrations, strongly depend on phytoplankton production

and its decomposition. As phytoplankton growth mainly depends on flow and light conditions in rivers (Chapter 2), future climate change will probably alter phytoplankton dynamics. Climate change is assumed to lead to changes in global radiation, air temperature, wind velocity, relative humidity and cloud cover which lead to changes in discharge conditions (IPCC 2007). In addition to changes in the total quantity of annual and seasonal rainfall, climate change may influence the occurrence and dynamics of individual extreme events (Johnson et al. 2009). Some studies suggest that in European freshwater ecosystems, the occurrence of extreme meteorological conditions, like increased precipitation in winter or heat waves in summer, will increase (Schär et al. 2004; Stott et al. 2004). Extremely high water temperatures in summer could cause shifts in phytoplankton species composition and stimulate primary production. Higher precipitation may enhance the probability of floods and induce changes in discharge leading to altered sediment budgets, changes in the amount of suspended substances and higher habitat disturbance frequency (Whitehead et al. 2009). Phytoplankton production is low during flood events which reduce the light availability and lead to poor growth conditions for phytoplankton. Low flow conditions improve the light climate in the water column and reduce the dilution capacity of rivers for sewage effluents and therefore increase the risk of eutrophication (Hilton et al. 2006). Hence, low flow conditions present favorable conditions for a high phytoplankton production.

As stream water temperature tracks air temperature (Langan et al. 2001; Mouthon and Daufresne 2006), the water temperature of streams and rivers is expected to increase due to the projected climate change. All chemical and biological processes of a river system depend on the water temperature, hence this is a central water quality parameter. For instance, rising water temperatures may result in considerably higher biochemical oxygen consumption rates (Sand-Jensen and Pedersen 2005) or may influence the whole biocoenosis of a water course (Daufresne et al. 2007). Higher water temperatures could alter phytoplankton amounts in the river, due to stimulation of phytoplankton production and changes in loss rates and food web interactions.

The problem in investigating the effects of climate change on aquatic ecosystems is the complexity and the multitude of changing factors. To combine climatologic, hydrological, morphological and anthropogenic impacts on river water quality, models are a useful tool to simulate possible scenarios for the future and to consider mitigation options. To assess the impact of climate change on water quality, modeling approaches and process based models

are useful tools. Dynamic, mechanistic models are particularly suitable for the simulations of water quality, because they allow the analysis of interactions between different processes (De Angelis and Mooij 2003; Ellner and Guckenheimer 2006). Water quality models can be applied to changing biotic and abiotic factors, like water temperature, average light level or discharge. In order to trace the development of riverine phytoplankton, models require an accurate depiction of hydrological processes at temporal and spatial scales (Sellers and Bukaveckas 2003; Williams 2006). Model simulations can also be used to advise management options for controlling eutrophication and mitigating possible negative effects of anthropogenic intervention, like heated effluents. Therefore, several attempts to realize predictions of riverine phytoplankton by simulation models were performed in different regulated and unregulated rivers (Everbecq et al. 2001; Scharfe et al. 2009; Quiel et al. 2011; Descy et al. 2012). Modeling possible consequences of climate change on the Rhine ecosystem is necessary to help answering open questions about future states of its water quality and navigability and to consider mitigation options.

Present study

Climate change effects on the phytoplankton development in the river Rhine were investigated in a multi model approach. Representative model chains were selected from a model assemblage consisting of 20 realizations of global and regional climate projections based on different CO_2 emission scenarios (IPCC 2007). They represented climate projections for the near (2021 – 2050) and the far future (2071 – 2100) in comparison to an assigned reference period (1961 – 1990). The modeled river stretch from kilometer 359 to 865 encompassed the majority of the free-flowing part of the river (Fig. 4.1). Simulations were performed with the water quality simulation model QSim of the Federal Institute of Hydrology – BfG (Kirchesch and Schöl 1999). The deterministic and process-based model QSim is composed of modules concerning hydraulic, physical, chemical, and biotic processes and was already applied to several river systems including the Rhine and the Elbe (Schöl et al. 1999; Schöl et al. 2002; Becker et al. 2010; Quiel et al. 2011). For the actual application, the model area was completely reestablished on the basis of current morphological profiles.

With the newly established model, simulations of different climate projections were performed and the following hypotheses were tested:

i) Climate change associated water temperature increases enhance riverine phytoplankton amounts.

ii) Low discharge events as a consequence of climate change positively affect phytoplankton biomass in rivers.

iii) Changes in global radiation due to climate change can change the concentrations of river phytoplankton.

Fig. 4.1: The red line represents the free-flowing part of the Rhine in Germany from Rhine-km 336 to 865. Karlsruhe is situated at the Upper Rhine (Rhine-km 362), Koblenz at the Middle Rhine (Rhine-km 590) and Bimmen at the Lower Rhine (Rhine-km 865).

4.3 Methods

Study area

The source of the Rhine is Lake Toma in the Swiss Alps. With a total length of 1,250 km, the Rhine is among the longest rivers in central Europe. The catchment area is 185,260 km² and the mean discharge (MQ) at Emmerich (Lower Rhine at the Dutch-German border, Rhine-km 852) is 2,300 m^3 s^{-1} (Uehlinger et al. 2009). While the upper section of the Rhine is characterized by several impoundments, the lower one beginning at Rhine-km 336 is free-flowing with a mean water depth of 3 – 5 m and a mean width of 400 m. The so called Upper Rhine, from Basel (Rhine-km 150) to Bingen (Rhine-km 530) includes the major tributaries Neckar (MQ = 140 m^3 s^{-1}) and Main (MQ = 224 m^3 s^{-1}) and is surrounded by vast industrial areas. The river reach from Bingen (Rhine-km 530) to Bonn (Rhine-km 660) designates the Middle Rhine which cuts through the Middle Rhine Mountains, with the main tributary Moselle (MQ = 329 m^3 s^{-1}). At the river banks of the Lower Rhine from Bonn (Rhine-km 660) to Lobith (Rhine-km 865), the large cities Cologne and Düsseldorf are situated, and some smaller tributaries flow into the Rhine. As the Rhine forms the major navigable waterway for transportation, it is economically one of the most important rivers in Europe. The numerous industrial facilities and power plants of this densely populated area involve ecological consequences of thermal pollution from heated discharges and wastewater treatment effluents. Recently, the chlorophyll *a* concentrations in the Rhine declined, for instance at Lobith, annual mean chlorophyll concentrations decreased from 26 µg L^{-1} (average 1977 – 1981) to 11 µg L^{-1} (average 2001 – 2005) (Uehlinger et al. 2009). At the station Koblenz (Rhine-km 590), seasonal mean (March to October) chlorophyll values decreased from 22 µg L^{-1} in 1990 to 1 µg L^{-1} in 2009 (cf. Chapter 2, Fig. 2.2).

Water quality simulation model QSim

The water quality simulation model QSim calculates longitudinal profiles and seasonal cycles of water quality parameters including phytoplankton biomass along a river reach (Schöl et al. 1999). In the present study, it was used to investigate climate change effects on phytoplankton development, oxygen content, and water temperature of the Rhine. QSim is a deterministic, one dimensional, mathematical model. For the Rhine, a spatial resolution of 500 meter and a

temporal resolution of one hour was applied. The water quality calculation with QSim is based on the hydraulic model Hydrax that calculates discharge conditions on the basis of cross-sectional profiles (Oppermann 1989). These two submodels, one for the hydraulic parameters and the other for the biological parameters are joined in a single graphical user interface (GUI) called Gerris (Dr. Schumacher, Ingenieurbüro für Wasser und Umwelt – IWU). QSim is an adequate tool to model climate change impacts on water quality, because it is composed of several modules describing different processes of an ecosystem. The modules describe hydraulic, physical, chemical, and biotic processes and therefore complex interactions between the different processes are taken into account (Kirchesch and Schöl 1999). The model results are annual courses of, for instance, plankton dynamics, nutrient concentrations, oxygen budgets or water temperature development. The model QSim was continuously used and refined by the Federal Institute of Hydrology (BfG) for questions concerning the water quality in Federal Waterways. By means of QSim, Quiel et al. (2011) investigated several projections of regional climate change on the river Elbe to simulate future trends of climatic and socioeconomic conditions. QSim was applied to the rivers Moselle and Saar in order to model the influence of benthic filter feeders on phytoplankton (Schöl et al. 1999) and the effect of thermal stratification in the river Saar (Becker et al. 2010). The Rhine was modeled with a focus on phytoplankton in the scope of an intensive monitoring program of the Rhine in 1990 including plankton and macrozoobenthos (Schöl et al. 2002).

Model setup Rhine

The GUI GerrisGME and Gerris include the model coupling of QSim and Hydrax. GerrisGME serves to edit the bathymetry, thus the morphological frame of the model including profiles, subdivision of the river in sections, location of tributaries and the characteristics of other boundary conditions, like assignment of meteorological stations to the different river sections. Boundary conditions are the discharge at the start point of the model, the water-level at the end point and tributaries as well as influent streams along the entire river area. Gerris (current version 1.6 (3) used in the present study) thus provides the definition of the model with hydrological, climatologic, chemical and biological input data.

For the current application, the Rhine model was entirely reconstructed by processing cross-sectional profiles, using version 2.1.15 of the graphical model editor GerrisGME. The river reach was divided into four individual line sections each with approximately 100 kilometers

length which were connected via nodes to a coherent river net. River section one included Rhine-km 359 – 469.5, river section two Rhine-km 469.5 – 601.5, river section three Rhine-km 601.5 – 733.5 and river section four Rhine-km 733.5 – 865.5. In total, the model included the free-flowing, German river reach from Rhine-km 359 to Rhine-km 865, 11 tributaries (Table 4.2), as well as 16 thermal discharges from industrial and nuclear power plants (ICPR 2006, BUND 2009).

For the setup of the hydrological model, morphological profiles of river cross-sections at intervals of 500 m were derived from a digital terrain model (DTM, WSD West P-2004.prf). The profiles were converted from .prf format into .xyk format, the necessary format for the import into the model editor GerrisGME. In xyk format (x = horizontal width of the profile in meters, y = height of the profile in meters above sea level; k = River-km, determining the longitudinal placement of the profile), the profiles were used to establish the substructure for the hydrodynamic modeling with Hydrax. For calibration, the profiles were reprocessed in GerrisGME by determination of the main span keeping the majority of the river water and adjusting the roughness values (Manning-Strickler) of the bottom area of the profile. In order to distinguish different bottom currents, roughness values (k_{ST} in $m^{1/3}$ s^{-1}) of the main opening lay in the range of 30 – 45 $m^{1/3}$ s^{-1} for a smooth bottom area and roughness values of floodplains or side channels lay in the range of 12 – 25 $m^{1/3}$ s^{-1} for a rough bottom area. 70 % of the bottom area of the profile at mean water-level were assumed to belong to the river bottom area, whereas the remaining area was defined to be river bank and hence available for settlement by macrozoobenthos.

The hydrodynamic model Hydrax calculates hydrological parameters along the modeled river reach (discharge, water velocity, volume of the water, water-level) which are necessary for the subsequent water quality simulation runs. In the stationary model run, Hydrax calculates mean water-levels based on an intermediate discharge input value for each boundary condition. As input data for the hydrological model, daily discharge data were used at the boundaries, i.e. upper model boundary (Rhine-km 359) and tributaries, and water-level data were used at the lower model boundary (Rhine-km 865). Discharge and water-level data were derived from the Federal Waterways and Shipping Administration (WSV, provided by the BfG). Instationary model runs with Hydrax must be calculated for the water quality simulations with QSim. The water quality simulations provide for instance nutrient concentrations, suspended substances, oxygen concentration, water temperature, chlorophyll

concentration and algal composition. Parameters and constants used in the model, and references from the literature, are provided in Table 4.1.

QSim and input data

For the current application of water quality simulation in the Rhine, QSim version 13.00 was used. Input data for the water quality simulation (for start values and tributaries) and for the validation of the model were derived from regional authorities: the LANUV-NRW (Landesamt für Natur, Umwelt und Verbraucherschutz NRW), HLUG (Hessisches Landesamt für Umwelt und Geologie), LUBW (Landesanstalt für Umwelt, Messungen und Naturschutz Baden-Württemberg), LUWG (Landesamt für Umwelt, Wasserwirtschaft und Gewerbeaufsicht Rheinland-Pfalz), and from the ICPR.

For the definition of the current status of river water quality, the years 2000 and 2005 – 2008 were modeled. For the water quality model run, input data at the boundaries (start value at Karlsruhe Rhine-km 359 and 11 tributaries, see Table 4.2) were phytoplankton composition, zooplankton abundance and diverse water quality parameters (Schöl et al. 2002; Quiel et al. 2011). Information about mussel abundances and shipping traffic were included for each river section. Through the modular structure of the model, it is possible to represent different processes of, for instance, oxygen, nutrient or temperature budget. Input data for the main tributaries Neckar, Main, and Moselle were available for every modeled year, whereas input data from the smaller tributaries Nahe, Lahn, Ahr, Sieg, Wupper, Erft, Ruhr and Lippe were only available for the years 2005 – 2008. In the case of missing data which applied to the Ruhr in 2007 and 2008, data from the previous year were used instead. The input data for the year 2000 were available for the Neckar, the Main, and the Moselle.

Along the entire modeled river reach, three weather stations were chosen and assigned to the respective river sections: Karlsruhe (49°02’N, 08°21’E), Frankfurt am Main (50°02’N, 08°35’E) and Düsseldorf (51°17’N, 06°46’E). Climatologic input data were provided by the German Weather Service (DWD) and included the following parameters: minimum and maximum of air temperature (°C), wind velocity (m s^{-1}), relative humidity (%), global radiation (J cm^{-2} d^{-1}) and cloudiness (total coverage in eighth). Global radiation data were derived from the alternate stations Mannheim, Geisenheim and Bochum. Gaps in data series of global radiation were filled with 500 J cm^{-2} d^{-1} in winter and 1,000 J cm^{-2} d^{-1} in summer.

Table 4.1: Parameterization in QSim for algae and rotifers.

Process variable	Unit	Bacill.	Chloro.	Cyano.	Rotifera	Reference
Chlorophyll/ Biomass	µgChla $mgBio^{-1}$	21.5	21.5	21.5		Geider 1987
Max. growth rate	day^{-1}	1.6	1.8	1		Reynolds 1984
Temperature optimum	°C	20[a]	33.5[b]	26[c]	21[d]	Schöl et al. 2002[a]; Dauta 1982[b]; Bouterfas et al. 2002[b]; Nicklisch et al. 1992[c]; Gentile and Maloney 1969[c]; Straškraba and Gnauck 1983[d]
Half saturation constant N	mg L^{-1}	0.018	0.048	0.02	–	Calculated after Baird and Emsley 1999
Light saturation photosynthesis	µE m^{-2} s^{-1}	39	88	34		Evaluation of literature data by Volker Kirchesch (Harris 1978)
Max. cell quota N	mg $mgBio^{-1}$	0.1	0.049	0.085	–	Stoichiometric after Vollenweider 1985
Min. cell quota N	mg $mgBio^{-1}$	0.017	0.008	0.014	–	Ratio of max. N-content/ min. N-content after Roelke et al. 1999
Max. uptake rate N	day^{-1}	0.31	0.09	0.31	–	Calculated after Baird and Emsey 1999
Half saturation constant P	mg L^{-1}	0.02	0.022	0.02	–	Calculated after Baird and Emsley 1999
Max. cell quota P	mg $mgBio^{-1}$	0.009	0.012	0.007	–	Sommer 1994
Min. cell quota P	mg $mgBio^{-1}$	0.0011	0.0016	0.0009	–	Sommer 1994
Max. uptake rate P	day^{-1}	0.62	0.69	0.62	–	Calculated after Baird and Emsey 1999
Half saturation constant Si	mg L^{-1}	0.08	–	–	–	Calculated after Baird and Emsey 1999
Max. cell quota Si	mg $mgBio^{-1}$	0.18	–	–	–	Sommer 1991
Min. cell quota Si	mg $mgBio^{-1}$	0.18	–	–	–	Sommer 1991
Max. uptake rate Si	day^{-1}	2.5	–	–	–	Calculated after Baird and Emsey 1999
Min. respiration	day^{-1}	0.085	0.085	0.085	–	Schöl et al. 2002
C-BOD_5 of phytoplankton	mg $µgChla^{-1}$	0.021	0.004	0.004	–	Experimental results Volker Kirchesch (unpublished)
COD of phytoplankton	mg $µgChla^{-1}$	0.105	0.073	0.073	–	Experimental results Volker Kirchesch (unpublished)
Min. O_2 production	mg $mgBio^{-1}$	1.3	1.3	1.3	–	Stoichiometric after Vollenweider 1985, NH_4-N as N source
Max. O_2 production	mg $mgBio^{-1}$	1.8	1.8	1.8	–	Stoichiometric after Vollenweider 1985, NO_3-N as N source
Intensity of sedimentation	0 – 1	0.5	0.5	0	–	Experimental results Volker Kirchesch (unpublished)
Filterability	0 – 1	0.6	0.8	0.1	–	Rothhaupt 1990
Max. ingestion rate	µgC day^{-1}	–	–	–	2.9	Walz 1993; Rinke 2006
Half-saturation constant for C ingestion	mg L^{-1}	–	–	–	0.43	Hayward and Gallup 1976
Biomass (dry matter)	µg $ind.^{-1}$	–	–	–	0.3	Dumont et al. 1975
Basic respiration	day^{-1}	–	–	–	0.03	Canale 1976

Bacill. Bacillariophyceae, *Chloro.* Chlorophyceae, *Cyano.* Cyanophyceae, *C-BOD_5* carbonaceous biological O_2 demand in 5 days, *COD* chemical O_2 demand

Table 4.2: Model boundaries, model end point and mean discharge (MQ) at the boundaries. Data of MQ provided by the Federal Waterways and Shipping Administration (WSV).

River (gauging station)	Rhine-km	MQ ($m^3 s^{-1}$)
Start: Rhine (Maxau)	359	1,270 (1970 – 2010)
Neckar (Rockenau SKA)	428	140 (1970 – 2010)
Main (Raunheim)	496.5	224 (1980 – 2010)
Nahe (Grolsheim)	529	31 (1970 – 2010)
Lahn (Kalkofen)	585.5	45.8 (1970 – 2010)
Moselle (Cochem)	592.5	329 (1970 – 2010)
Ahr (Altenahr)	629	7.11 (1961 – 2006)
Sieg (Menden)	659	50.8 (1970 – 2009)
Wupper (Opladen)	702	14.9 (1970 – 2010)
Erft (Neubrück)	740	15.8 (1970 – 2010)
Ruhr (Hattingen)	780	70.6 (1970 – 2010)
Lippe (Schermbeck 1)	815	41.8 (1970 – 2010)
End: Rhine (Lobith)	865.5	2,250 (1970 – 2010)

Validation

The model parameters used in the present study are listed in Table 4.1 and were derived mainly from literature values (V. Kirchesch, personal communication; Quiel et al. 2011). Model results of the years 2000 and 2008 were validated at the measuring station Bimmen (Rhine-km 865) and the gauging station Lobith (Rhine-km 862) for the parameters chlorophyll *a*, oxygen, water temperature and discharge. The quality of the model results was tested by calculating the model efficiency (the so called Nash-Sutcliffe-Efficiency, NSE); and the relative error. The NSE compares the measured and the modeled values and tests how well the modeled values correspond to the measured values (Loague and Green 1991; Moriasi et al. 2007). Hence, the model efficiency provides the deviation from the 1:1 line. The results of the NSE can range between -∞ and +1, while the optimal fit is represented by 1.

$$NSE = \frac{1 - \sum (o - s)^2}{\sum (o - o_{mean})^2}$$

o = observed value

s = simulated value

o_{mean} = mean of the observed values

As the model efficiency is very sensitive towards single outliers, the relative error was additionally determined (Arhonditsis and Brett 2004). The relative error considers the overall model performance and the relative deviation of the modeled values with a minor impact of

outliers. If the relative error is equal to 0, the fit is optimal.

$$relative\ error\ =\ \frac{\sum|\ o-s\ |}{\sum o}$$

o = observed value

s = simulated value

Furthermore, a regression analysis was performed and the coefficient of determination of the linear regression between modeled and measured values (R^2) and the slope of the regression line (S) were considered. The optimum for R^2 and S is 1 which indicates identical modeled and measured values. A deviation from the slope of 1 reveals an over- or underestimation of the modeled values compared to the measured data.

Model chains

Within the scope of the research program KLIWAS (KLIWAS 2013), a 'Multi-model Ensemble' consisting of 20 realizations, i.e. combinations of different CO_2 emission scenarios (IPCC 2007), Global Climate Models (GCMs) and Regional Climate Models (RCMs) was provided based mainly on the results of the EU-project ENSEMBLES (ENSEMBLES-Partner 2009) and also on the project ZWEK (DWD 2008) and the EU-project PRUDENCE (Jacob et al. 2007). The DWD accomplished the downscaling of the climate model data for the Rhine river system from horizontal grids of 25 km to single meteorological stations. In combination with corresponding realizations of discharge projections for the Rhine (Nilson et al. 2010a), necessary input parameters for the water quality simulations were generated. Thus, the water quality calculations were based on climatological input data and on hydrological input data derived from the HBV 134 hydrological model over the catchments of the Rhine (Nilson et al. 2010b). From the KLIWAS 'Multi-model Ensemble', comprising several global and regional model chains, five representative climate model chains were chosen which covered a possible range (bandwidth) of future climate conditions for the Rhine river system. The representative model chains were chosen according to the indicator 'NM7Q' (lowest arithmetic mean discharge values during 7 days) for the hydrological summer (May to October) referring to the gauging station Kaub (Rhine-km 546). The selected model chains represented those chains with the highest and the lowest NM7Q projected for the near future (2012 – 2050) and the far

future (2071 - 2100) (cf. corridor of scenarios, Nilson et al. 2010b). An additional 'intermediate' chain was chosen because it represents global and regional models that are often used in climate impact research. The results can therefore be better evaluated and compared between different studies. The driving GCMs of the five climate model chains used in the present study are primarily ECHAM5 and HadCM3 based on the A1B emission scenario (ENSEMBLES-Partner 2009), and are listed in table 4.3.

Table 4.3: Five climate model chains chosen from the KLIWAS 'Multi-model Ensemble' to cover a possible range of future climate conditions based on the A1B emission scenario (IPCC 2007). Near future = 2021 – 2050; far future = 2071 – 2100. ECHAM5 = model of the Max-Planck-Institute for Meteorology (MPI; Roeckner et al. 2003); BCM = Bergen Climate Model (Furevik et al. 2003); HadCM3Q0/ HadRM3Q0 = model of the Hadley Centre (Johns et al. 2003); RCA3.0 = model of the Swedish Meteorological and Hydrological Institute (SMHI; Räisänen et al. 2004); REMO = model of the Max-Planck-Institute for Meteorology (MPI; Jacob 2001); RACMO2 = model of the Royal Netherlands Meteorological Institute (KNMI; Lenderink et al. 2003); CLM = model of the Institute for Coastal Research (GKSS; Steppler et al. 2003).

Period		Emission Scenario	Global Climate Model (GCM)	Regional Climate Model (RCM)
1. Intermediate for near and far future		A1B	ECHAM5 - Run3	REMO5.7
2. Near future	- upper boundary	A1B	BCM	RCA3.0
3. Near future	- lower boundary	A1B	HadCM3Q0	HadRM3Q0
4. Far future	- upper boundary	A1B	ECHAM5 - Run3	RACMO2.1
5. Far future	- lower boundary	A1B	ECHAM5 - Run1	CLM2.4.11

This so called 'multi model approach' of KLIWAS allowed to consider a potential range of future climatic developments by using several model chains. For each model chain, the reference period (1961 – 1990) was calculated additionally to the corresponding projection period (2021 – 2050 or 2071 – 2100).

Generation of input data for simulation calculations and the quantile mapping approach

Two projection periods were defined, the near future from 2021 to 2050 and the far future from 2071 to 2100. The simulations were performed by changing meteorological and hydrological input data and invariant water quality conditions, except water temperature.

Whereas all water quality input parameters remained invariant, the input data for water temperature at the model boundaries were adjusted to the ambient climatic conditions of the respective model chain. Therefore, the model QSim was used, which includes a module to calculate water temperature based on the climatologic parameters. Thus, the 'real' years 2000 and 2005 – 2008 were projected into the future with changed climatologic conditions. Along the Rhine, several power plants and industrial facilities lead their thermal discharges into the Rhine, evoking warmer river water temperatures. In order to produce a 'worst case' scenario, the maximal values of allowed cooling water input (yearly mean in values in MJ s^{-1} = MW y^{-1}) of the 16 largest dischargers along the Rhine were included (ICPR 2006, BUND 2009).

The 'quantile mapping approach' (Wood et al. 2002) was used to relate the past climate conditions to future climate projections. At first, a distribution function of the measured parameters sensitive to climate change (global radiation, air temperature, relative humidity, cloudiness, wind speed, discharge) was established. The time period defined as 'water quality reference period' was 1981 – 2010, because the available measured water quality data lay within the time span 2000 – 2010. A time span of 30 years is reasonable for climate change analysis, because climate acts on this time scale. Distribution functions relying on measured values for the water quality reference period (1981 – 2010) on the one hand, and for modeled values for the assigned reference period (1961 – 1990 and 1981 – 2010), for the near (2021 – 2050) and for the far future (2071 – 2100), on the other hand were established. By means of the 'quantile mapping approach', the measured climatologic and hydrologic values (for instance air temperature) of the water quality reference period (1981 – 2010) were aligned to the modeled values of the reference (1961 – 1990 and 1981 – 2010) and projection periods (2021 – 2050 or 2071 – 2100). Thus, each measured value from the water quality reference period was correlated to a certain sequence value (precision: 1000 steps) independent of the point in time. To each sequence value, a corresponding modeled value was assigned. This corresponding modeled value depended on the respective model chain.

For the simulation calculations of the years 2000 and 2005 – 2008, the modified climatologic input data were used for transferring the climate signal of the corresponding model chain.

4.4 Results

The validation results showed that discharge and water temperature dynamics were reproduced by the model with a good model-fit to measured data sets from the real system (Table 4.4; Fig. 4.2). For these physical variables, detailed input data on a daily basis were available and in 2008 at Rhine-km 865, the NSE for water temperature was 0.98, the relative error was 0.03, R^2 was 0.99 and the slope of the regression line (S) was 0.99. The validation results of water temperature included the maximal values of allowed cooling water input. In contrast, the modeled chlorophyll *a* and O_2 values showed stronger deviations from the measured values. This could be ascribed to incomplete input data, which were available on a biweekly basis and the more complex calculations needed for the simulations, that involved higher uncertainties and more assumptions.

Table 4.4: Model validation results: Model efficiency as Nash-Sutcliffe-efficiency (NSE), relative error, coefficient of determination (R^2) and slope (S) of the linear regression between modeled and measured values for the state variables chlorophyll *a* (Chl *a*), oxygen (O_2), discharge (Q) and water temperature (WT) for the years 2000 and 2008 at Bimmen (Rhine-km 865).

	NSE		**Relative error**		***R²***		**Slope (S)**	
Year	2000	2008	2000	2008	2000	2008	2000	2008
Chl *a*	0.888	0.379	0.316	0.844	0.867	0.456	0.884	1.175
O_2	-0.816	0.918	0.229	0.191	0.770	0.507	1.200	1.118
Q	0.938	0.959	0.054	0.045	0.948	0.960	0.911	0.987
WT	0.978	0.980	0.050	0.030	0.960	0.990	0.986	0.986

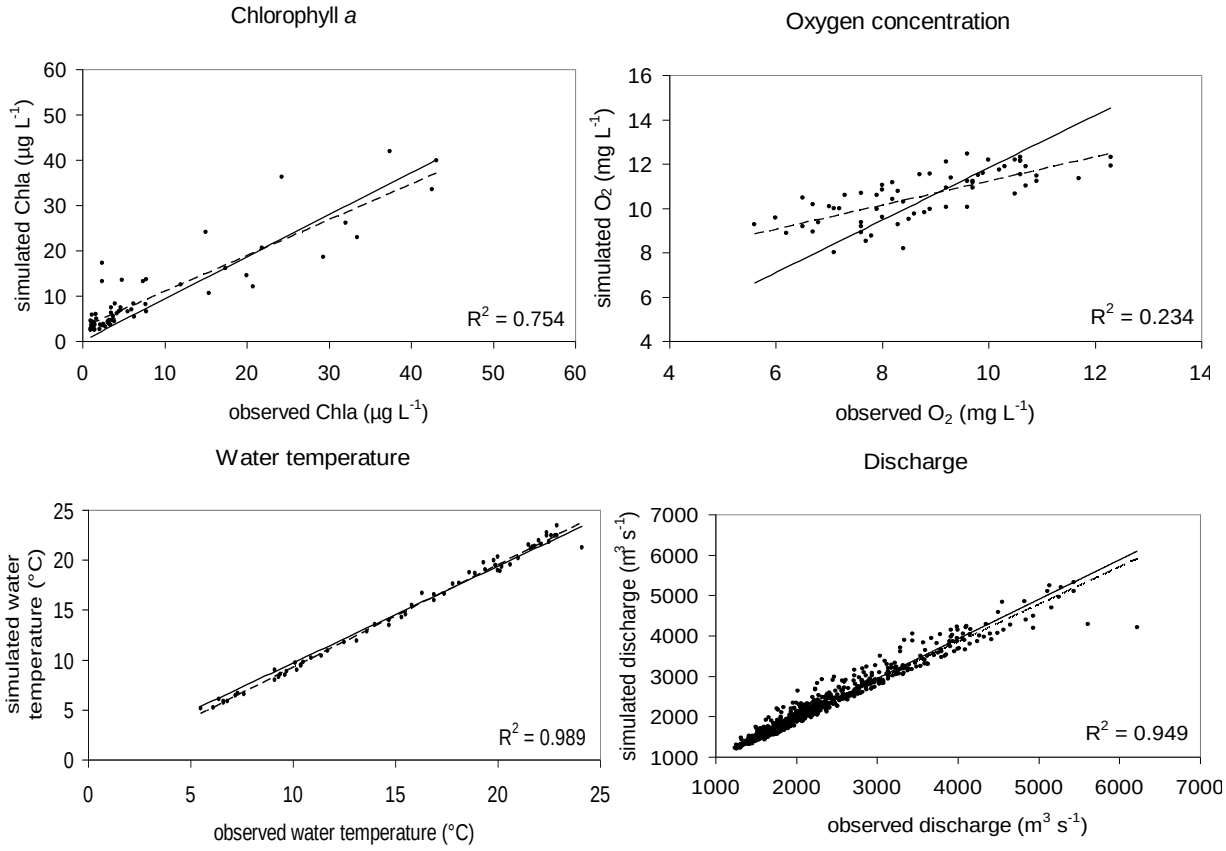

Fig. 4.2: Model validation results for the years 2000 and 2008 at Bimmen (Rhine-km 865): simulated versus observed values for the parameters chlorophyll *a*, oxygen concentration, water temperature and discharge. Dashed line represents optimal fit, black line represents the 1:1 line with the corresponding R^2, the coefficient of determination.

The mean value for global radiation increased in all model chains in the near future compared to the reference period from 1,038 J cm^{-2} d^{-1} to 1,041 J cm^{-2} d^{-1}, and decreased in the far future to 1,022 J cm^{-2} d^{-1} (Table 4.5). As for the input data of air temperature, the mean air temperature of all model chains decreased in the near future compared to the reference period from 12.4°C to 12.2°C and increased in the far future to 14.0°C. The highest mean air temperature increase of + 1.9°C could be found for the model chain of the lower boundary of the far future (from 12.5°C to 14.4°C) while the lower boundary of the far future revealed an increase of + 1.3°C (from 12.5 to 13.8). The start values of mean discharge increased from 1,220 m^3 s^{-1} in the reference period to 1,242 m^3 s^{-1} in the near future, whereas it slightly decreased in the far future to 1,217 m^3 s^{-1} (Table 4.6). All minimum discharges of the tributaries and the minimum start values decreased in the far future compared to the reference.

Table 4.5: Changes in input parameters for global radiation and air temperature: For one model chain, the annual mean and median values of the climatologic input data are presented. The values of the three meteorological stations of the same model chain were averaged.

		Global radiation		Air temperature	
Model chains		**Mean**	**Median**	**Mean**	**Median**
1 Ref	- intermediate	1,045	777	12.1	12.1
2 Ref near future	- upper boundary	1,021	877	11.8	12.0
3 Ref near future	- lower boundary	1,069	906	12.9	13.0
4 Ref far future	- upper boundary	1,059	849	12.5	12.7
5 Ref far future	- lower boundary	997	708	12.5	12.1
Reference mean		**1,038**	**823**	**12.4**	**12.4**
1 Near future	- intermediate	1,031	761	11.9	11.9
2 Near future	- upper boundary	1,017	865	11.6	11.8
3 Near future	- lower boundary	1,076	924	13.1	13.2
Near future mean		**1,041**	**850**	**12.2**	**12.3**
1 Far future	- intermediate	1,013	743	13.7	13.3
4 Far future	- upper boundary	1,050	817	13.8	13.4
5 Far future	- lower boundary	1,005	713	14.4	13.6
Far future mean		**1,022**	**758**	**14.0**	**13.4**

Table 4.6: Changes in input parameters for discharge: For one model chain, annual mean and minimum values are presented. Minimum discharges at the start point (Rhine-km 359) and the tributaries of each simulated year were averaged.

Discharge		**Rhine (start)**		**Neckar**		**Main**		**Moselle**	
		Mean	Min	Mean	Min	Mean	Min	Mean	Min
1 Ref	- intermediate	1,231	489	134	27	211	74	344	30
2 Ref near future	- upper boundary	1,202	576	127	30	194	70	319	43
3 Ref near future	- lower boundary	1,225	518	137	24	216	73	348	27
4 Ref far future	- upper boundary	1,224	514	134	26	212	70	341	26
5 Ref far future	- lower boundary	1,220	541	132	31	204	79	339	47
Reference mean		**1,220**	**528**	**133**	**28**	**207**	**73**	**338**	**35**
1 Near future	- intermediate	1,200	537	137	30	220	72	333	42
2 Near future	- upper boundary	1,309	649	146	35	240	86	356	44
3 Near future	- lower boundary	1,217	492	131	17	219	66	337	16
Near future mean		**1,242**	**559**	**138**	**27**	**226**	**75**	**342**	**34**
1 Far future	- intermediate	1,222	490	155	20	254	67	378	14
4 Far future	- upper boundary	1,307	500	164	16	268	63	385	7
5 Far future	- lower boundary	1,122	423	140	15	226	57	349	12
Far future mean		**1,217**	**471**	**153**	**17**	**249**	**62**	**371**	**11**

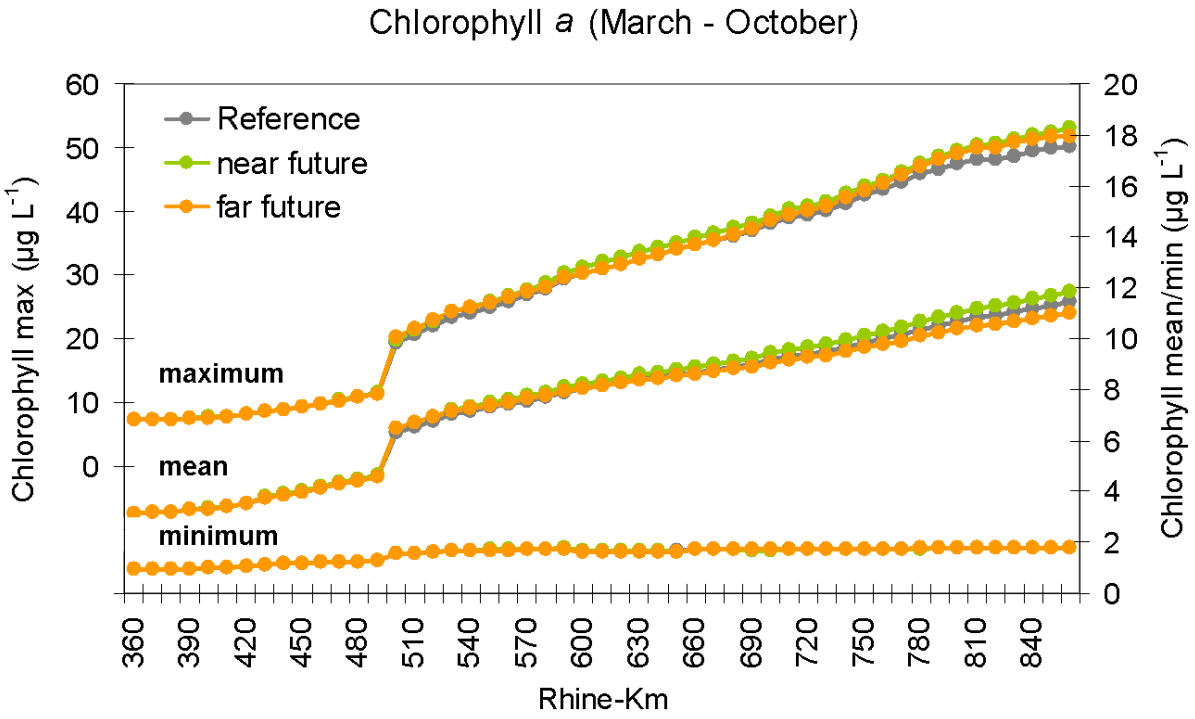

Fig. 4.3: Simulation results of the intermediate climate model chain (1) for chlorophyll: development of maximum, mean and minimum chlorophyll *a* values presented as mean over the vegetation period (March – October). For the determination of maximum and minimum values, the values of each simulated year were averaged. Grey lines represent the reference period, green lines the near future and red lines the far future.

Table 4.7: Simulation results of all model chains (1 – 5) for chlorophyll: Mean over the vegetation period (March – October), maximum and minimum of chlorophyll *a* for each model chain at Koblenz (Rhine-km 590) and Bimmen (Rhine-km 860). For the determination of maximum and minimum values, the values of each simulated year were averaged.

Chlorophyll *a*		**Mean**	**Mean**	**Max**	**Max**	**Min**	**Min**
Reference		Kobl.	Bimmen	Kobl.	Bimmen	Kobl.	Bimmen
1 Ref	- intermediate	7.89	11.48	29.38	50.53	1.74	1.79
2 Ref near future	- upper boundary	8.07	12.15	30.08	53.47	1.73	1.82
3 Ref near future	- lower boundary	8.02	11.58	30.02	51.53	1.79	1.93
4 Ref far future	- upper boundary	7.94	11.49	29.21	49.73	1.77	1.91
5 Ref far future	- lower boundary	7.74	11.00	29.50	49.48	1.72	1.81
Near future							
1 Near future	- intermediate	8.09	11.91	30.22	53.28	1.76	1.77
2 Near future	- upper boundary	7.90	11.45	28.54	49.63	1.75	1.87
3 Near future	- lower boundary	8.03	11.78	29.82	53.03	1.78	1.94
Far future							
1 Far future	- intermediate	7.94	11.03	29.57	51.82	1.73	1.77
4 Far future	- upper boundary	7.50	10.50	27.95	47.89	1.70	1.88
5 Far future	- lower boundary	8.04	11.03	31.56	53.70	1.75	1.86

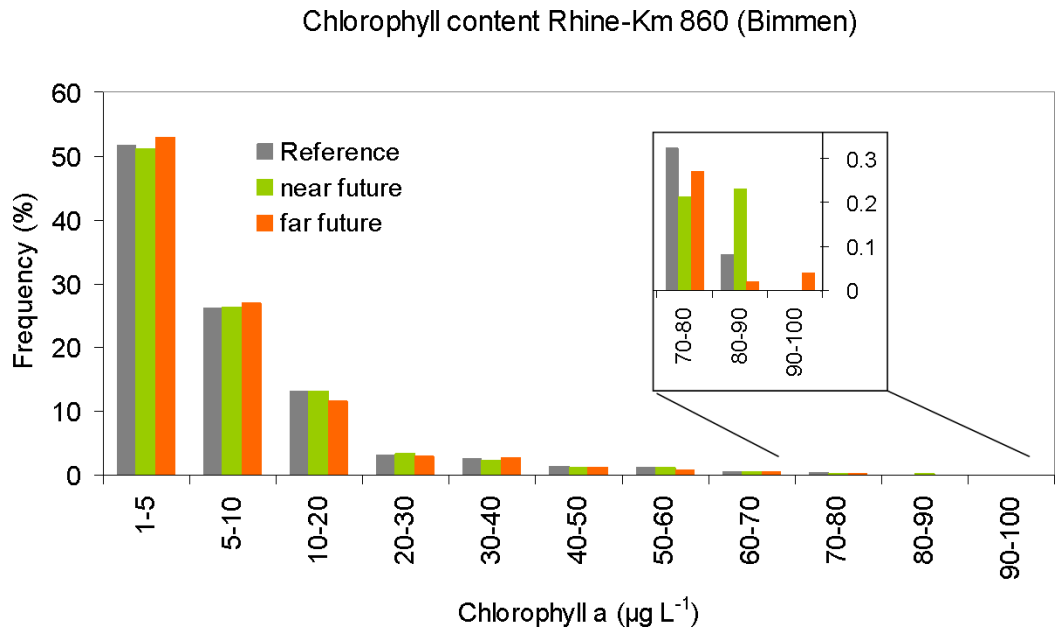

Fig. 4.4: Frequency distribution of the chlorophyll content at Rhine-km 860. Results of the values of all model chains (1 – 5) for the reference period (1961 – 1990), the near future (2021 – 2050) and the far future (2071 – 2100).

The model results of the intermediate model chain (chain 1) indicated that the mean chlorophyll *a* values increased downstream the Rhine and that this increase was slightly less pronounced for the period of the far future compared to the reference period leading to lower mean values at the end of the modeled river reach (Rhine-km 860) (Fig. 4.3). By contrast, maximal values were higher in the far future at the end of the modeled river reach.

The comparison of the results of all model chains (chains 1 – 5) revealed that the model chain of the lower boundary for the far future (chain 5) produced the strongest changes in chlorophyll development. The strongest increase in chlorophyll values of + 4.22 µg L^{-1} could be detected at Rhine-km 860, here maximal chlorophyll values increased from 49.48 µg L^{-1} in the reference period to 53.70 µg L^{-1} in the far future (Table 4.7).

The frequency distribution at Bimmen (Rhine-km 860) including the values of all model chains (chains 1 – 5) showed that lower chlorophyll values of 1 – 5 µg L^{-1} were more frequent in the far future (Fig. 4.4). By contrast, high values in the range of 90 – 100 µg L^{-1} only occurred in the far future and were absent in the near future and the reference period.

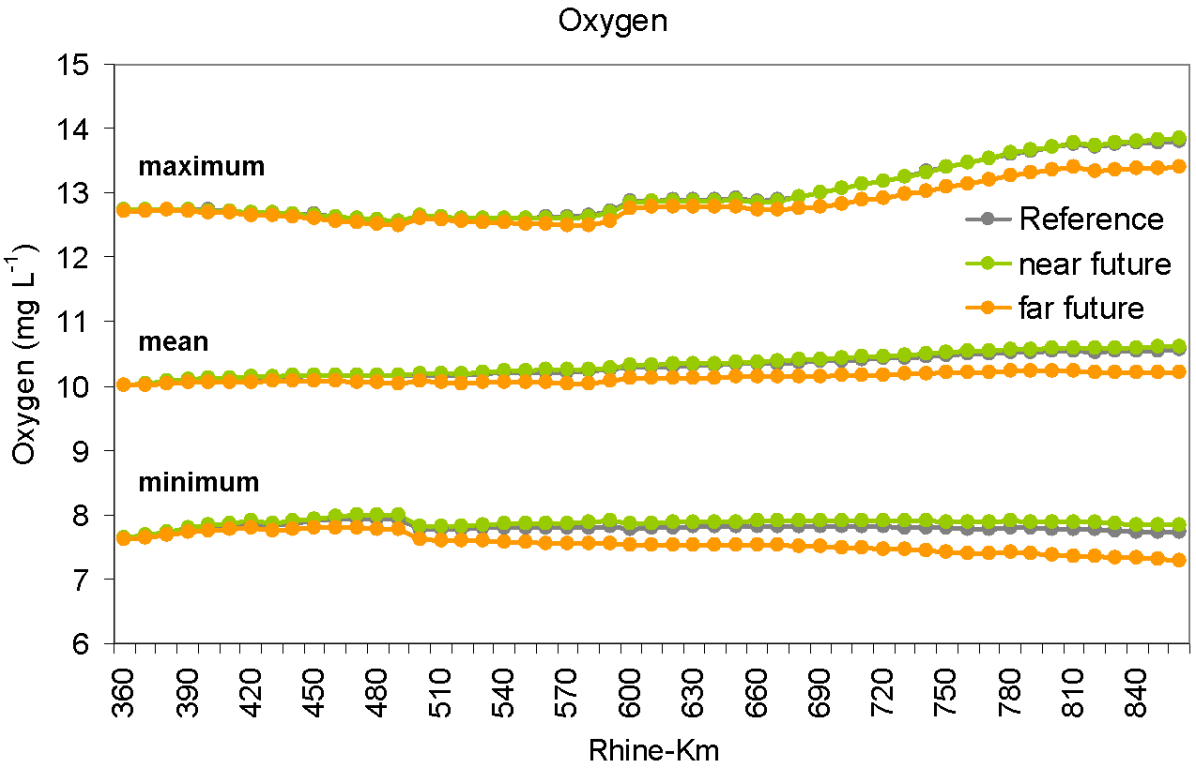

Fig. 4.5: Simulation results of the intermediate climate model chain (1) for oxygen: development of maximum, mean and minimum oxygen values presented as annual mean. For the determination of maximum and minimum values, the values of each simulated year were averaged. Grey lines represent the reference period, green lines the near future and red lines the far future.

Table 4.8: Simulation results of all model chains (1 – 5) for oxygen: Annual mean, maximum and minimum of oxygen concentration for each model chain at Koblenz (Rhine-km 590) and Bimmen (Rhine-km 860). For the determination of maximum and minimum values, the values of each simulated year were averaged.

Oxygen		**Mean**	**Mean**	**Max**	**Max**	**Min**	**Min**
Reference		Kobl.	Bimmen	Kobl.	Bimmen	Kobl.	Bimmen
1 Ref	- intermediate	10.3	10.6	12.7	13.8	7.8	7.7
2 Ref near future	- upper boundary	10.3	10.6	12.5	13.9	8.1	8.1
3 Ref near future	- lower boundary	10.2	10.4	12.6	13.7	7.6	7.5
4 Ref far future	- upper boundary	10.2	10.4	12.6	13.6	7.8	7.6
5 Ref far future	- lower boundary	10.2	10.5	12.7	13.8	7.6	7.5
Near future							
1 Near future	- intermediate	10.3	10.6	12.7	13.9	7.9	7.8
2 Near future	- upper boundary	10.3	10.6	12.6	13.6	8.1	8.2
3 Near future	- lower boundary	10.1	10.3	12.5	13.7	7.7	7.5
Far future							
1 Far future	- intermediate	10.1	10.2	12.6	13.4	7.6	7.3
4 Far future	- upper boundary	10.0	10.2	12.5	13.3	7.5	7.3
5 Far future	- lower boundary	10.0	10.1	12.4	13.3	7.3	7.0

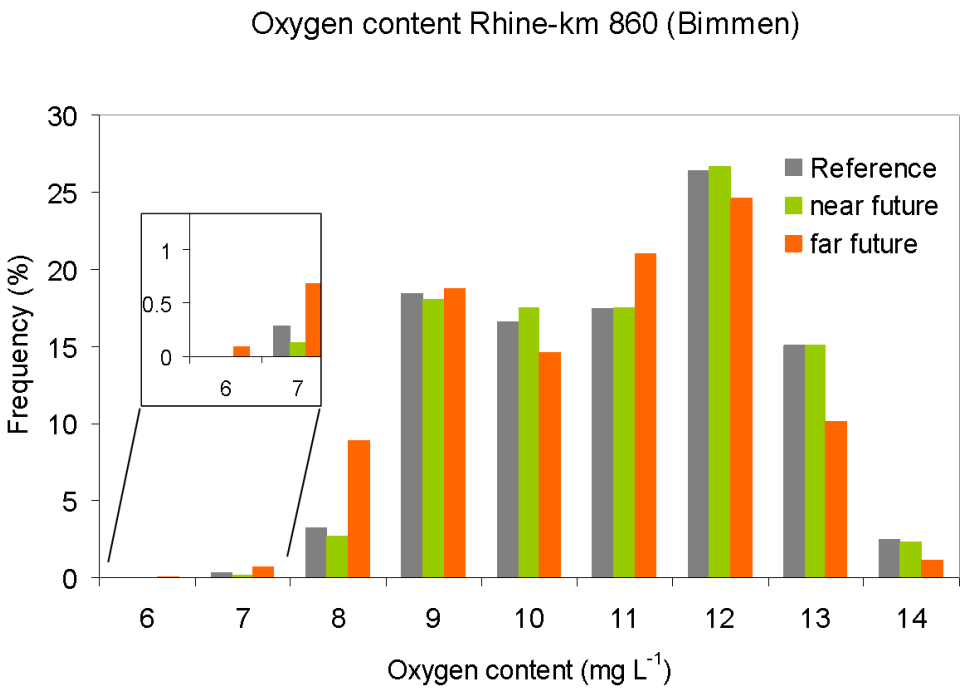

Fig. 4.6: Frequency distribution of the oxygen content at Rhine-km 860. Results of the values of all model chains (1 – 5) for the reference period (1961 – 1990), the near future (2021 – 2050) and the far future (2071 – 2100).

For the intermediate model chain (chain 1), the mean oxygen concentration decreased in the far future compared to the reference period and to the near future (Fig. 4.5). Likewise, this decrease in the far future was observed for the maximum and the minimum values.

Among all model chains (chains 1 – 5), oxygen concentrations decreased in the far future (Table 4.8). The strongest mean oxygen decrease of - 0.4 mg L^{-1} could be detected at the end of the river reach (Rhine-km 860) for the lower boundary of the far future (chain 5). Here, the mean oxygen concentration decreased from 10.5 mg L^{-1} in the reference period to 10.1 mg L^{-1} in the far future. At the same location, the oxygen minimum values decreased from 7.5 in the reference period to a minimum of 7.0 mg L^{-1} in the far future (Δ - 0.5, chain 5).

The frequency distribution of the oxygen values derived from all model chains (1 – 5) at Bimmen demonstrated an increase of values in the lower range of 7 – 8 mg L^{-1} for the far future (Fig. 4.6). The frequency of higher values in the range of 13 – 14 mg L^{-1} decreased in the far future compared to the near future and the reference period.

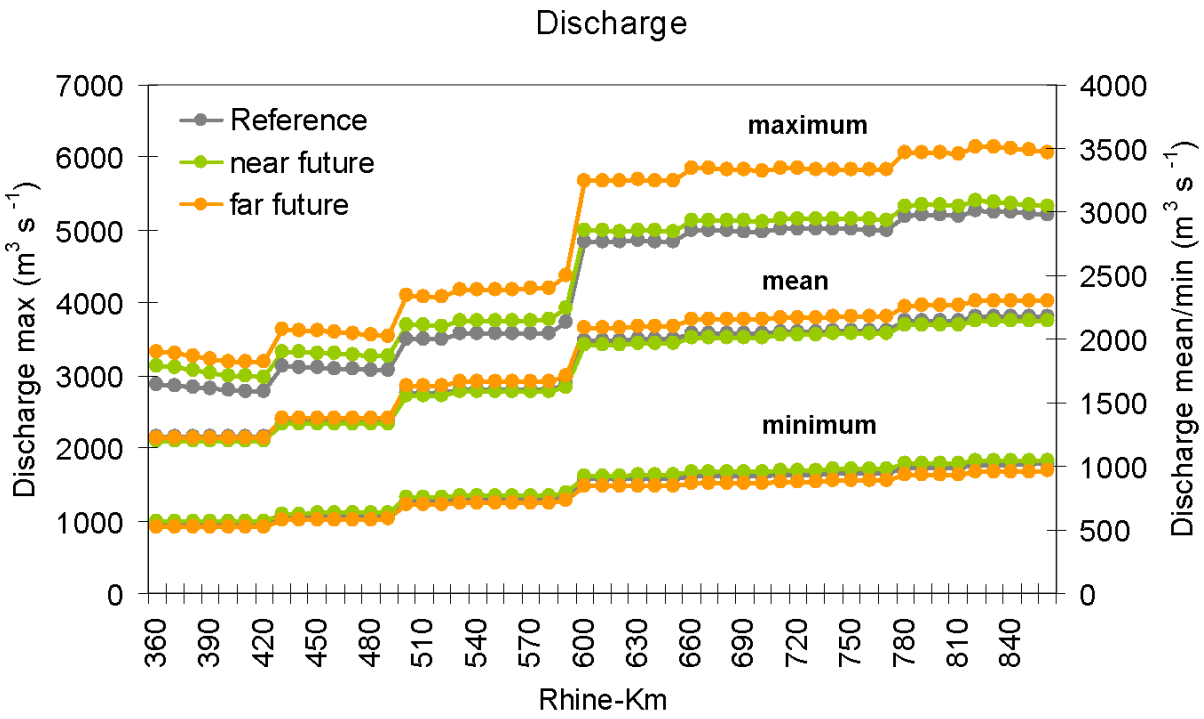

Fig. 4.7: Simulation results of the intermediate climate model chain (1) for discharge: development of maximum, mean and minimum discharge values presented as annual mean. For the determination of maximum and minimum values, the values of each simulated year were averaged. Grey lines represent the reference period, green lines the near future and red lines the far future.

Table 4.9: Simulation results of all model chains (1 – 5) for discharge: Annual mean, maximum and minimum discharge for each model chain at Koblenz (Rhine-km 590) and Bimmen (Rhine-km 860). For the determination of maximum and minimum values, the values of each simulated year were averaged.

Discharge		**Mean**	**Mean**	**Max**	**Max**	**Min**	**Min**
Reference		Kobl.	Bimmen	Kobl.	Bimmen	Kobl.	Bimmen
1 Ref	- intermediate	1,646	2,174	3,590	4,872	758	1,018
2 Ref near future	- upper boundary	1,588	2,081	3,733	4,864	807	1,075
3 Ref near future	- lower boundary	1,649	2,183	3,947	5,257	772	1,029
4 Ref far future	- upper boundary	1,641	2,165	3,857	5,170	756	1,021
5 Ref far future	- lower boundary	1,626	2,144	3,829	5,162	789	1,054
Near future							
1 Near future	- intermediate	1,627	2,142	3,788	4,958	789	1,044
2 Near future	- upper boundary	1,773	2,326	4,102	5,402	917	1,188
3 Near future	- lower boundary	1,638	2,161	4,074	5,401	715	966
Far future							
1 Far future	- intermediate	1,716	2,298	4,202	5,673	733	962
4 Far future	- upper boundary	1,828	2,425	4,713	6,404	742	975
5 Far future	- lower boundary	1,566	2,105	4,127	5,587	642	854

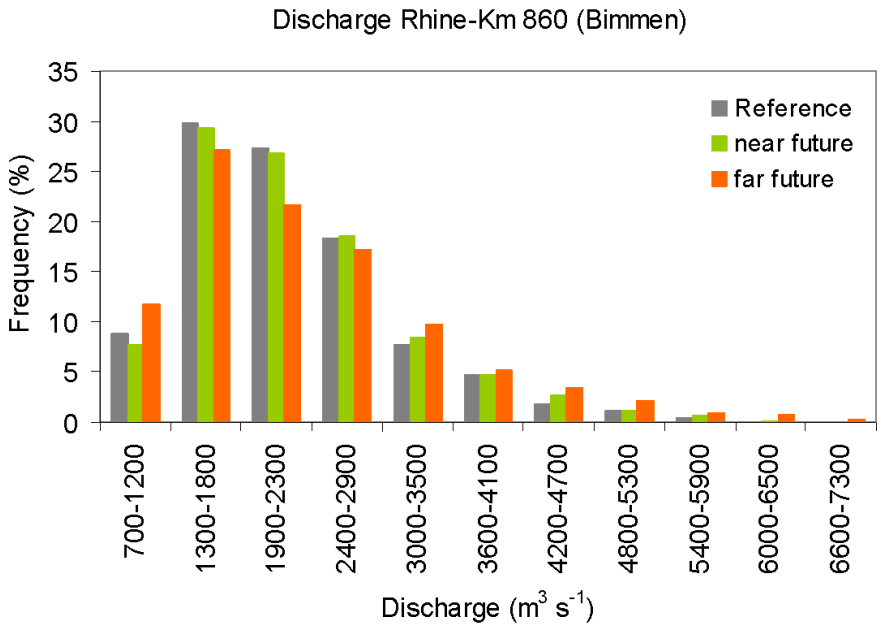

Fig. 4.8: Frequency distribution of the discharge at Rhine-km 860. Results of the values of all model chains (1 – 5) for the reference period (1961 – 1990), the near future (2021 – 2050) and the far future (2071 – 2100).

Within the intermediate model chain (chain 1), the mean discharge slightly increased in the far future compared to the reference period and the near future which did not differ much from each other (Fig. 4.7). Whereas the minimum discharge slightly decreased in the far future, the maximum values increased by about 1,000 $m^3 s^{-1}$ at the end of the modeled river reach (Rhine-km 860). The impact of the tributaries is apparent from a stepwise increase of discharge values downstream. The comparison of all model results (chains 1 – 5) showed that within the results of the lower boundary of the far future (chain 5), the discharge decreased compared to the reference period at Koblenz and Bimmen (Table 4.9). The results for the upper boundary of the far future (chain 4) revealed increasing discharge conditions compared to the reference period for both stations. Within the model chain for the lower boundary of the far future (chain 5), maximum discharge at the end of the river reach increased from 5,162 $m^3 s^{-1}$ in the reference period to 5,587 $m^3 s^{-1}$ (Δ + 425 $m^3 s^{-1}$). The minimum values decreased from 1,054 $m^3 s^{-1}$ in the reference period to 854 $m^3 s^{-1}$ in the far future (Δ - 200 $m^3 s^{-1}$, chain 5). The frequency distribution of discharge for all model chains (chains 1 – 5) at the station Bimmen revealed increases in the frequency of lower values between 700 – 1,200 $m^3 s^{-1}$ for the far future (Fig. 4.8). Intermediate discharges in the range from 1,300 – 2,900 $m^3 s^{-1}$ decreased in the far future compared to the near future and the reference period, whereas higher values above 3,000 $m^3 s^{-1}$ occurred more frequently in the far future.

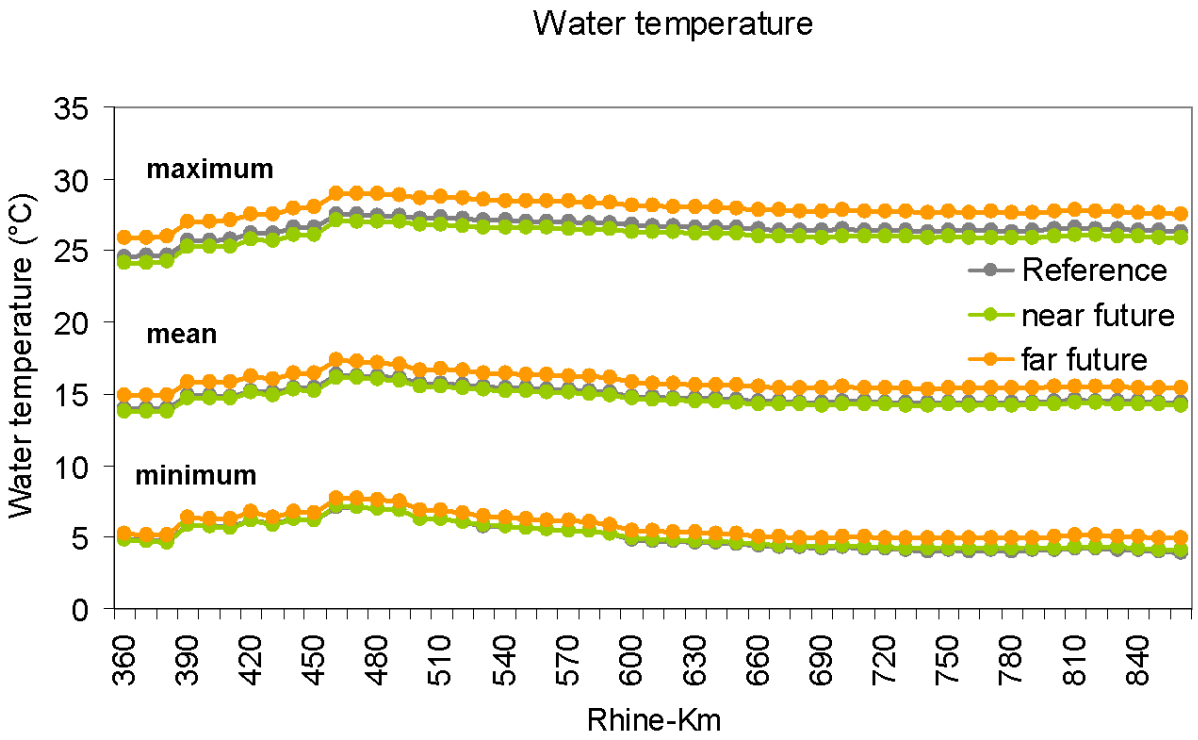

Fig. 4.9: Simulation results of the intermediate climate model chain (1) for water temperature: development of maximum, mean and minimum water temperature presented as annual mean. For the determination of maximum and minimum values, the values of each simulated year were averaged. Grey lines represent the reference period, green lines the near future and red lines the far future.

Table 4.10: Simulation results of all model chains (1 – 5) for water temperature: Annual mean, maximum and minimum of water temperature for each model chain at Koblenz (Rhine-km 590) and Bimmen (Rhine-km 860). Rhine-km 460 was included to show maximal water temperature which was highest at this location. For the determination of maximum and minimum values, the values of each simulated year were averaged.

Water temperature		**Mean**	**Mean**	**Max**	**Max**	**Min**	**Min**
Reference		Kobl.	Bimmen	Kobl./ 460	Bimmen	Kobl.	Bimm.
1 Ref	- intermediate	15.1	14.3	26.9/ 27.5	26.3	5.2	3.9
2 Ref near future	- upper boundary	14.9	14.2	25.3/ 26.0	24.6	5.8	4.6
3 Ref near future	- lower boundary	15.7	15.0	27.9/ 28.5	27.0	5.7	4.6
4 Ref far future	- upper boundary	15.5	14.8	27.2/ 27.8	26.7	5.7	4.6
5 Ref far future	- lower boundary	15.2	14.3	28.0/ 28.8	27.0	5.3	4.4
Near future							
1 Near future	- intermediate	14.9	14.2	26.4/ 27.1	25.8	5.2	4.1
2 Near future	- upper boundary	14.7	14.0	24.9/ 25.5	24.3	5.7	4.6
3 Near future	- lower boundary	15.8	15.1	27.8/ 28.4	26.9	6.0	4.9
Far future							
1 Far future	- intermediate	16.1	15.3	28.3/ 29.0	27.5	5.9	4.9
4 Far future	- upper boundary	16.3	15.6	28.6/ 29.2	27.9	6.1	5.3
5 Far future	- lower boundary	16.5	15.6	29.5/ 30.6	28.5	6.4	5.6

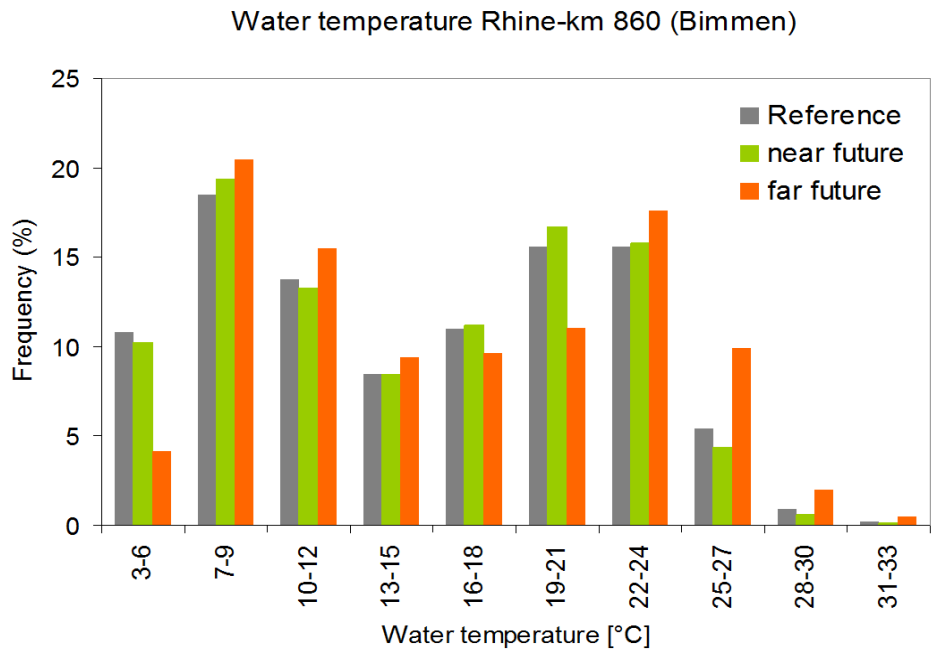

Fig. 4.10: Frequency distribution of the water temperature at Rhine-km 860. Results of the values of all model chains (1 – 5) for the reference period (1961 – 1990), the near future (2021 – 2050) and the far future (2071 – 2100).

In the longitudinal development, strongest increases of water temperature could be observed between Rhine-km 360 to 460 (Fig. 4.9). The results of the intermediate model chain indicate that the water temperature increased in the far future and the most pronounced increases were present in the maximum values. The maximum, mean and minimum water temperatures increased in the far future compared to the reference period and to the near future which were in a similar range.

The comparison of all simulation results (chains 1 – 5) revealed that water temperatures increased in all model chains in the far future (Table 4.10). Mean water temperature increases of + 1.3°C were found for the lower boundary of the far future (chain 5) at Koblenz. Mean water temperature increased from 15.2°C in the reference period to 16.5°C in the far future. The highest maximal water temperatures were 29.5°C and 30.6°C in the far future (chain 5) at Koblenz and Rhine-km 460, respectively. At these locations, the maximal water temperatures were 28.0°C and 28.8°C in the reference period, hence the maximal increase was + 1.8°C.

The frequency distribution of water temperatures including all model values (chains 1 – 5) revealed that high water temperatures above 25°C occurred much more frequently in the far future compared to the reference period and the near future (Fig. 4.10).

4.5 Discussion

Validation

The results of the validation demonstrated that physical parameters can be simulated with a higher accuracy compared to biological parameters, due to the higher complexity of biological processes. A good model fit is indicated by high values of model efficiency and low values of relative errors. For oxygen in 2000, model efficiency was low, but the relative error was in an acceptable range. Within a meta-study including several recent mechanistic aquatic models, a mean relative error of 0.12 for oxygen was indicated (Arhonditsis and Brett 2004), and in the present study the relative error was in the range of 0.19 and 0.22. For water temperature Arhonditsis and Brett (2004) found mean relative errors of 0.07, while in the present study relative errors were lower with 0.03 and 0.05. They indicated a mean relative error for chlorophyll of 0.44, and in the present study relative errors of 0.31 and 0.84 were found.

Input parameters

In the climate projections, annual mean global radiation increased only slightly in the near future and showed a decreasing trend in the far future. A decreasing global radiation in the far future might weaken the increase in water temperature and diminish phytoplankton growth due to a less favorable light climate under water. It was reported that in addition to air temperature, increases in global radiation can have a strong impact on future water temperatures (Haag 2009). However in the present study, the changes in input parameters of global radiation were small.

Annual mean air temperature increased in the far future compared to the reference period. A mean air temperature increase of + 1.8°C to + 2.3°C was assumed for Germany in the far future (2071-2100) based on the regional model WETTREG, the global model ECHAM5 and the emission scenarios B1 (‘moderate’), A1B (‘intermediate’) and A2 (‘extreme’) (UBA 2007a; UBA 2007b). In the present study, using the A1B scenario (IPCC 2007), mean air temperature increase for the far future compared to the reference period was in the range of + 1.3°C to + 1.9°C (see Table 4.5). Water temperature tracks air temperature with a shift of about 2 days. This reaction time can be explained by the limited heat exchange capacity of water and depends on water depth (Erickson and Stefan 2000). Therefore, increases in water temperature are likely to occur congruent to air temperature increases.

The annual mean discharge slightly increased for most model chains in the near future and decreased in the far future for the start values. Minimum discharge values of the main tributaries and of the start point decreased in the far future compared to the reference period. In Southern Europe, models revealed decreasing precipitation as a consequence of climate change, whereas in Northern Europe, increasing precipitation was assumed (Hagemann and Jacob 2007). According to Christensen et al. (2007), projections of changes in precipitation vary highly. In the Rhine, the contribution of tributaries in terms of discharge is high, and they can strongly influence the total discharge of the main river, especially during low flow conditions. Increasing discharge conditions could diminish phytoplankton development, whereas decreasing discharge conditions, especially during spring, could enhance phytoplankton development (cf. Chapter 2).

Simulation calculations

The simulation results of the near future (2021 – 2050) were very similar to the results of the reference period (1961 – 1990), therefore the focus of the discussion was set mainly on the development in the far future (2071 – 2100) where the effects were stronger. For the far future, strongest effects were predominantly found for the lower boundary, represented by model chain 5 and the results discussed below refer mainly to this model chain. In order to project future trends, the discussion focuses on changes (Δ) between reference and future periods and not on absolute values.

Maximum values of chlorophyll *a* (mean over the vegetation period: March to October) slightly increased in the near and the far future compared to the reference period at Bimmen (Rhine-Km 860). A change in mean values of chlorophyll could hardly be detected and also the changes in maximum values were relatively small in the far future (maximum increase at Bimmen: $\Delta + 4.22\ \mu g\ L^{-1}$; chain 5).

The mean, maximum and minimum water temperature increased in the far future compared to the reference period. The maximal water temperature increase was most pronounced at Rhine-km 460 (Δ + 1.8°C; chain 5) compared to Rhine-km 865 (Δ + 1.5°C; chain 5). This increase could be mainly attributed to the air temperature increase of the input data. The effect of the water temperature increase was reflected in the minimum oxygen concentration which decreased in the far future compared to the reference period due to a lower solubility

(decrease at Bimmen: Δ - 0.5 mg L^{-1}; chain 5). Furthermore, increased water temperature could partly cause the increases in maximum chlorophyll values (hypothesis i). As these increases were very small, other processes seemed to prevail. The pronounced stepwise increase in water temperature from Rhine-km 360 to 460 could be explained by thermal discharges derived from power plants and industrial facilities which are very high within this river reach. In the present study, the maximal allowed amounts of cooling water input of 16 industrial facilities were included in all water quality simulations (ICPR 2006, BUND 2009). Downstream Rhine-km 460, the impact of these thermal discharges became smaller and was less pronounced at Rhine-km 865. It is difficult to separate the pure impact of climate change from the anthropogenic impacts of urbanization and industrial heat input by cooling water discharge which can artificially change the natural river water temperature (Meier et al. 2003; Webb et al. 2008). Since 1900, the water temperature of the Rhine has increased about + 3°C, whereof + 2°C were assumed to rely on industrial heat exchange water and only + 1°C were assumed to be caused by climate change (Peñailillo et al. 2008). Furthermore, these authors report an increased frequency of days with water temperatures above 25°C which is congruent to the results of the present study. In Germany, the maximal allowed water temperature subsequent to input of heated discharges by industrial facilities is 28°C. When the mixed temperature reaches this limit, the input of heated discharges into the river must be down-regulated, in order to protect fish and fauna (Gerstengarbe and Werner 2007; Koop et al. 2007). Hence, the use of maximal thermal discharges for the simulations is an overestimation (worst case scenario) considering future rises in water temperatures.

In the present study, minimum discharge at Bimmen decreased (Δ - 200 m^3 s^{-1}; chain 5) in the far future compared to the reference period. This decrease of 20 % was probably the reason for the increases observed in chlorophyll maxima, because longer water residence times present favorable growth conditions (hypothesis ii). On the other hand, within the same model chain for the far future, maximum discharge values at Bimmen were higher compared to the reference period (Δ + 425 m^3 s^{-1}, chain 5). For the upper boundary of the far future, represented by model chain 4, the increase in maximum discharge values was even more pronounced with an increase of 24 % compared to the reference period at Bimmen (Δ + 1,234 m^3 s^{-1}, chain 4). Hence, in model chain 4, the increase in discharge maxima exceeded the decrease in the discharge minima and the mean discharge values at Bimmen exceeded the reference by 12 % in the far future. Additionally to the strength of the changes in discharge,

the timing of low flow conditions during the year is crucial for the effect on phytoplankton growth (cf. Chapter 2). For the Rhine, projections of a multi-model approach, from which the projections of the present study were derived, indicated a reduction of discharge in summer and an increase of discharge in winter for the 'far future' 2071 – 2100 (Nilson et al. 2010b). Therefore, the low discharge in summer should have an effect on phytoplankton, while the higher discharge in winter hardly influences phytoplankton which occurs in low concentrations in winter. As shown in Chapter 2, the hydrological situation in spring strongly influences the phytoplankton dynamics in the Rhine and determines the development of a spring phytoplankton bloom. It can therefore be concluded that the future development of the hydrograph in spring and of summer low flow situations will have the most pronounced influence on phytoplankton dynamics. A negative effect of increased flow conditions on phytoplankton growth due to shorter residence times and a poor light climate in the water column was observed in simulations of the Seine River and the Elbe (Garnier et al. 1995; Quiel et al. 2011).

In the present study, the impact of global radiation was assumed to be negligible, because changes in input values were very small. Moreover, changes in cloud cover which was also included in the model could interfere with the strength of global radiation reaching the water surface. Therefore, it was concluded that the impact of global radiation was not strong enough to change phytoplankton concentrations (hypothesis iii).

Altogether, the response of water quality parameters, especially in phytoplankton biomass was weak towards changes in climatic variables. This weak response could be due to the choice of climate projections based on the intermediate emission scenario A1B (IPCC 2007). A more extreme emission scenario with more pronounced changes in climatologic conditions, like higher air temperatures or lower precipitation and lower flow conditions would probably provoke stronger responses of phytoplankton. Furthermore, it can be speculated that climate change effects on phytoplankton might be compensated by complex regulation mechanism including benthic filter feeders in the Rhine which could be able to reduce high phytoplankton amounts. In the model, grazing impacts on phytoplankton were exerted by zooplankton and mussels which were included in a simplified manner. The effect of *Dreissena polymorpha* which is implemented in the model was investigated by Schöl et al. (2002) and they confirmed the importance of interrelations of planktonic communities with river benthos. In the present modeling approach, the grazing rate of *Dreissena polymorpha* did not increase

with temperature in the far future, and should therefore not be the reason for the weak response of phytoplankton. Further research is needed to assess the magnitude of the impact of benthic grazers, for instance by incorporating *Corbicula fluminea* in the model. As grazing by benthic filter feeders might interact with changes in flow or temperature in multiple ways, the food web regulation prevailing in the Rhine ecosystem might compensate the direct effects of climate change. Possibly, these food web effects could compensate the positive, growth stimulating effects of low flow conditions on phytoplankton production. Several studies confirmed that the filtration activity of benthic filter feeders in the Rhine can be enhanced by higher water temperatures and the fitness can be improved by higher winter water temperatures (Viergutz et al. 2007; Weitere et al. 2008). Low flow conditions might strengthen the bentho-pelagic coupling and therefore the grazing pressure exerted on phytoplankton. Hence in the field, the effect of climate change may be mediated by indirect food web changes which could superimpose the direct effects of climatic conditions. Water quality simulations can provide valuable information about direction and magnitude of possible changes in river systems, but the picture of the future may be incomplete and includes a certain level of uncertainty. Furthermore, the response towards climate change strongly depends on river system properties. In the Elbe, a more pronounced effect of climate change on phytoplankton biomass was found using the A1B emission scenario (IPCC 2007) and a model chain that led to extreme discharge reductions (Quiel et al. 2011). These authors simulated extreme changes in flow input data (mean values from daily data, April to October) at the upper model boundary of up to – 44 % deviation from the reference and found changes in chlorophyll concentrations of more than 100 µg L^{-1}. Climate related flow reductions might have a stronger impact on phytoplankton development in the Elbe where the phytoplankton biomass is not exposed to stronger grazing by benthic filter feeders during low flow conditions.

It can be concluded that in the present modeling approach, the river system was weakly affected by changes in discharge, water temperature or global radiation. The small changes in phytoplankton biomass could be explained by relatively small changes in discharge reductions. It can be speculated that biotic interactions could to a certain degree compensate changes in phytoplankton biomass in response to climate change. Other river ecosystems with different regulation mechanisms and less pronounced food web effects might react stronger towards changing climatic conditions.

5 General discussion

Results of this study address open questions in phytoplankton regulation mechanisms in large rivers including past trends in biomass, recent short-term longitudinal dynamics and simulation calculations of future developments of water quality. Three different approaches on plankton dynamics in the rivers Rhine and Elbe are presented. The first approach is a statistical analysis of long-term chlorophyll data and different abiotic physicochemical parameters at single measuring stations from both rivers. The long-term data sets (Rhine: 1990 – 2009, Elbe: 1994 – 2009) were analyzed with the aim of detecting trends in phytoplankton biomass and identifying the most important regulation factors of spring bloom dynamics (Chapter 2). The second approach provides new aspects to the spatial plankton development downstream the Rhine and the Elbe and focuses on the short-term development. It was realized by performing longitudinal profiles downstream both rivers at different seasons (recent years: 2009 – 2011) and particular attention was paid to specific growth and loss processes during downstream transport (Chapter 3). The third approach presents model results of water quality parameters derived from a newly established and validated model of the river Rhine. The aim was to define possible future states of important water quality parameters of the Rhine ecosystem, like phytoplankton and water temperature. By means of QSim, the water quality simulation model of the BfG, a model area of the free-flowing part of the Rhine was established and simulation calculations were performed based on different climate projections for the near and for the far future (near future: 2021 – 2050; far future: 2071 – 2100) (Chapter 4). This model is open to further extensions and can be modified by other scientists who may use it for other purposes.

The analysis of long-term data revealed that in the Rhine (at Rhine-km 590, measuring station Koblenz) seasonal mean (March – October) phytoplankton biomass decreased significantly from 1990 to 2009, whereas in the Elbe (at Elbe-km 312, measuring station Magdeburg) a tendency towards increasing phytoplankton biomass could be detected from 1994 to 2009 (cf. Chapter 2; Fig. 2.2). At the beginning of the 1990s, seasonal mean chlorophyll values in the Rhine reached 37 µg L^{-1} at Koblenz, while during the last decade highest seasonal mean chlorophyll values were below 10 µg L^{-1}. During the longitudinal profile performed in May 2011, however, extremely high chlorophyll concentrations occurred in the Rhine, indicating that in the Rhine phytoplankton still has the potential to reach a high biomass. The realization

of this potential was obviously restricted by other processes prevailing during the last decade. Despite high nutrient concentrations in both rivers, higher seasonal mean chlorophyll values of 90 – 116 µg L^{-1} were regularly reached in the Elbe in recent years. While the Rhine is characterized by a low chlorophyll *a*/TP ratio, this ratio is high in the Elbe (Mischke et al. 2011). Thus, in the Elbe, nutrients are effectively incorporated into phytoplankton biomass. In the Rhine, loss processes are probably more important. A possible explanation of phytoplankton losses in the Rhine are the benthic filter feeders *Dreissena polymorpha* which extended since the 1970s and *Corbicula fluminea* which invaded the Rhine since the 1990s (Friedrich and Pohlmann 2009). Strong interactions of plankton and benthic filter feeders in rivers, especially during low flow conditions, were reported before (Cohen et al. 1984; Caraco et al. 2006; Schmidlin and Baur 2007). Hence, reductions in discharge may strengthen the bentho-pelagic coupling and the effect of grazing on phytoplankton may increase (Welker and Walz 1998). In the Elbe, plankton reduction via benthic filter feeding is low due to generally low abundances of bivalves.

In the present study, the decrease in phytoplankton biomass coincided with an earlier occurrence of the phytoplankton spring maximum in the Rhine. The timing of maximum light availability and the timing of discharge decrease partly controlled the spring bloom dynamics. Likewise, in mesocosm experiments, light appeared to play an important role in the initiation of the phytoplankton spring bloom (Sommer and Lengfellner 2008; Lewandowska and Sommer 2010). By contrast, no shift in the occurrence of the spring bloom could be found in the Elbe (cf. Chapter 2; Fig. 2.3). Here, the timing of the peak spring biomass coincided with the timing of decreasing discharge conditions. Hence, the decrease of the discharge peak in spring could be identified to be a prominent regulating factor of phytoplankton mass developments which present the food basis for organisms on higher trophic levels. In spring, a reduction in discharge leads to lower water-levels and to a favorable light climate in the water column promoting phytoplankton growth. Other studies confirmed the importance of discharge conditions, especially in combination with a long water residence time and a high light availability for the development of planktonic organisms (Reynolds 1995; Lucas et al. 2009). A negative correlation between discharge and chlorophyll has frequently been reported (Neal et al. 2006; Van Vliet and Zwolsman 2008; Ďesortová and Punčochář 2011) and spring flood decline was related to changes in phytoplankton species compositions (Romanov and Kirillov 2012). Measurements of under water light climate in relation to discharge in the

Great Ouse River showed that the onset of the spring bloom was determined by the discharge pattern (Marker and Collett 1997) and in the river Seine, phytoplankton development in spring was initiated by the decrease of flow (Garnier et al. 1995). Light conditions may exert a considerable influence on river phytoplankton development and often restrict phytoplankton growth, because of high turbulence and often turbid conditions in many rivers (Descy and Gosselain 1994; Koch et al. 2004).

The present study demonstrated that the factors water temperature and nutrient concentrations did not correlate with river phytoplankton biomass in spring, and underlines the assumption that nutrient concentrations are sufficient for phytoplankton growth in both rivers. This stands in contrast to the situation in lakes and other studies emphasizing the importance of these factors in rivers (Basu and Pick 1996; Van Nieuwenhuyse and Jones 1996). In lakes, the formation of a shallow mixed upper water layer generated by temperature induced vertical stratification is important for the development of a phytoplankton bloom (Gaedke et al. 1998) and nutrients are often the limiting resource (Winder and Sommer 2012). A time shift in phytoplankton blooms which developed one month earlier in spring was also observed in shallow lakes in response to shorter ice cover periods in winter, hence warmer water temperatures from 1979 – 1998 (Gerten and Adrian 2000). That means that in lotic waters different regulation mechanisms prevail, and the main focus has to be set on discharge conditions and light availability, whereas water temperature is probably of less importance. Hence, it can be suggested that water temperature plays a minor role in rivers compared to lakes. Mesocosm experiments revealed that responses of phytoplankton productivity mainly depended on other factors than temperature and that the timing of the spring bloom showed little response to warming (Sommer and Lengfellner 2008; Lewandowska et al. 2012). Lewandowska et al. (2012) concluded that temperature rather induced species shifts, smaller cell sizes and changes in community structure. For instance, in stagnant water bodies, a shift towards a dominance of cyanobacteria was frequently observed as a consequence of warmer water temperatures (Adrian and Deneke 1996). Long-term observations in a lake and model results revealed that the effect of irradiance, next to vertical mixing, has a main effect on spring bloom dynamics under climate change (Tirok and Gaedke 2007). Hence, light is obviously of particular importance for phytoplankton growth, both in lakes and in rivers. In rivers, favorable light conditions are induced by low discharge conditions (Koch et al. 2004), while temperature-induced vertical stratification enhances the light availability for

phytoplankton in lakes (Berger et al. 2007). A similarity between lakes and rivers in terms of nutrient concentrations is that an increase in nutrients, particularly phosphorus, is a prerequisite for eutrophic conditions to develop (Hilton et al. 2006). The present findings indicate that climate related factors, like discharge or light conditions, have a high potential to regulate phytoplankton spring bloom dynamics in rivers. Such a dependence could be an important tool for predicting phytoplankton development under climate change (Chapter 4). Nevertheless, the importance of biotic regulation factors should be kept in mind and further analysis including biotic factors in addition to abiotic factors could be useful.

Short-term developments during downstream transport in the Rhine indicated a strong net growth in the 1990s with high phytoplankton densities and strong longitudinal increases in chlorophyll *a* (Friedrich and Pohlmann 2009), but more recently, studies showed for phytoplankton only small, if any, net increases along the river (Scherwass et al. 2010). Despite small net increases of phytoplankton biomass along the river, possibly strong phytoplankton growth rates still prevail which are counterbalanced by strong loss processes due to grazing (Weitere and Arndt 2002). During the Lagrangian sampling campaigns performed in the present study, chlorophyll concentrations in the Rhine were low with maximal values below 5 µg L^{-1} in September 2010, but extremely high with up to 244 µg L^{-1} at Rhine-km 854 in May 2011 (cf. Chapter 3; Fig. 3.3). During the phytoplankton mass development of the spring peak in May 2011, chlorophyll concentrations exceeded the values measured during the last three decades and the observed trend of decreasing chlorophyll values in recent years was not continued (cf. Chapter 2). In the Elbe, chlorophyll reached maximal values of 120 µg L^{-1} in August 2011 and 180 µg L^{-1} in September 2009 at the end of the free-flowing part of the river (Elbe-km 560). Chlorophyll values in the order of 190 to 220 µg L^{-1} are frequently observed at the end of the free-flowing part of the Elbe (data: RBC Elbe). According to the measurements of the abiotic parameters, neither light nor nutrient limitation prevailed during the longitudinal sampling campaigns (cf. Chapter 3; Table 3.1, Table 3.2). The survey of macrozoobenthos in 2011 indicated high abundances of the invasive bivalves *Corbicula* sp. and *Dreissena* sp. in the Rhine in contrast to lower abundances in the Elbe. The high abundances of benthic bivalves found in the Rhine could be one possible reason for the decreasing plankton biomass observed in the Rhine in recent years. But the present study demonstrated that high production rates of phytoplankton during favorable low discharge and high light conditions still have the potential to compensate prevailing loss

processes so that exceptional conditions may lead to a pronounced regime shift. This means that the positive effect of low flow conditions on phytoplankton growth can make up for the negative effect of grazing by benthic filter feeders including bivalves.

Tributaries had contrasting effects in the two rivers. They provided an additional and important source of phyto- and zooplankton biomass and suspended matter in the Rhine, whereas they mostly diluted the plankton concentrations in the Elbe. In the Rest-Rhine (Rhine-km 291) and in the tributary Moselle Cryptophyceae presented a high fraction of total phytoplankton biovolume. Cryptophyceae are commonly favored in areas of lower water flow rates, conditions prevailing in the downstream sections or in impounded rivers (Bahnwart et al. 1998). In the Rhine this phytoplankton class was mainly contributed from the impounded tributaries. The Havel influenced the phytoplankton community in the downstream section of the Elbe by the input of Cyanophyceae which are frequently encountered in slower flowing waters. Concerning the zooplankton composition, the tributaries of the Rhine frequently carried mussel larvae (veliger larvae of *Dreissena polymorpha*), while in the tributaries of the Elbe mussel larvae were rarely found. Despite strong impacts of tributaries, river-internal processes seem to govern the characteristic plankton dynamics in the main rivers. Further research should quantify the potential phytoplankton growth rate with the exclusion of benthic filter feeders (bottle experiments) to estimate loss rates of plankton to the benthos (see Weitere and Arndt 2002 for an approach for heterotrophic nanoplankton).

Simulation calculations of water quality parameters based on climate projections for the near (2021 – 2050) and the far future (2071 – 2100) performed in the present study (by changing the climatic and hydrological input data of the model) revealed small changes in chlorophyll concentrations (Chapter 4). For the far future, chlorophyll increased maximally at the end of the free-flowing part of the Rhine (Δ + 4.22 µg L^{-1} at Rhine-km 860). A stronger effect could be observed in the model results for water temperature for the far future which increased along the entire river. According to the results of the long-term analysis, the direct effect of water temperature plays a minor role in phytoplankton mass developments, whereas the light climate is more important (Chapter 2). Compared to the reference period, water temperature increased maximally at Rhine-km 460 (Δ + 1.8°C). This increase could mainly be attributed to the increased air temperature projected for the far future which is expected to increase between + 1.4 to + 5.8°C until 2100 (IPCC 2007). The observed increase in water temperature could partly be the reason for the slight increase in maximum chlorophyll values. Water

temperature increases in the far future also explained the lower oxygen concentrations which decreased slightly in the far future (Δ - 0.5 mg L^{-1} at Rhine-km 860). The long residence time and the turbulence of the river water in the Rhine favors the heat exchange with the atmosphere and the alignment of air temperature to water temperature is enhanced with longer water residence times. On the other hand, there is a latitudinal gradient in air temperature from North to South, leading to slightly lower air and water temperatures in the northern section of the Rhine. At the northern station at Rhine-km 860, the water temperature difference between the far future compared to the reference period was + 1.5°C, hence water temperature increase was lower compared to the southern station at Rhine-km 460.

Model results of discharge indicated a decrease in minimum values for the far future at Bimmen (Rhine-km 860) which probably led to the increases observed in chlorophyll maxima. Likewise, projections of a multi-model approach, from which the projections of the present study were derived, indicated a reduction of discharge in summer for the 'far future' (2071 – 2100; Nilson et al. 2010b). Several studies predict changes in the discharge regimes of rivers due to climate change (Weiland et al. 2012). As demonstrated in the present study, discharge reductions in spring can have a strong influence on phytoplankton development (Chapter 2), while in the modeling approach of the present study, the overall response of phytoplankton biomass towards changes in climatic variables was weak. The long-term analysis of phytoplankton development demonstrated, that in the Rhine, discharge reduction influenced the timing of spring bloom events rather than the magnitude of total phytoplankton biomass which was probably prone to biotic regulation mechanisms (Chapter 2). It can further be hypothesized that high water temperatures earlier during the year might stimulate filtration activity of benthic filter feeders further reducing the magnitude of the phytoplankton spring bloom. The investigations of phytoplankton dynamics in the longitudinal profile revealed that net increases along the Rhine were small, strongly indicating loss processes (Chapter 3). On the other hand, it was shown that if phytoplankton production reaches a certain threshold level, induced by extraordinarily favorable growth conditions, a regime shift can occur in the Rhine, but this was an exception (Chapter 3). It is important to note that modeling can help to elucidate the mechanisms behind the observations from the field. The advantage of a modeling approach is that the interaction of different factors can be represented and it is furthermore possible to manipulate single factors in order to elucidate the response of the ecosystem. A further research task could be to perform simulation calculations of the Rhine

with and without the two most important benthic filter feeding bivalves *Dreissena polymorpha* and *Corbicula fluminea*, to test if the effects of climatic variables would change. Probably, recent changes in ecosystem properties of the Rhine play a crucial role to explain a weak response of phytoplankton towards changes in climatic variables in the field. The Rhine is a river system with strong anthropogenic impacts of thermal discharges derived from industrial facilities and power plants which is reflected in strong water temperature increases in the Upper Rhine. It is difficult to separate the pure impact of climate change from the anthropogenic impacts of urbanization and industrial heat input by cooling water discharge which can artificially change the natural river water temperature (Meier et al. 2003; Webb et al. 2008). In the scope of further climate-related water temperature increases, reductions in thermal discharges will be necessary to counterbalance massive water temperature increases. Consequences of water temperature increases on the ecosystem can be severe. The Rhine ecosystem for instance is already affected by the invasion of neozoan bivalve species (*Corbicula* sp. and *Dreissena* sp.) exerting a strong grazing impact on the phytoplankton. Improvements of water quality since the beginning of the 1970s promoted the spread out of these bivalves in the Rhine. While low flow conditions present favorable growth conditions for phytoplankton, they might strengthen the bentho-pelagic coupling and increase the grazing pressure (cf. Weitere and Arndt 2002). On the one hand, favorable light conditions might stimulate phytoplankton growth (Winder and Sommer 2012), on the other hand filtration activity and fitness of benthic filter feeders can be enhanced by higher water temperatures (Viergutz et al. 2007; Weitere et al. 2008). Hence, it is possible that climate change affects water quality indirectly by inducing food web changes. These indirect effects of climate change can interfere with and counterbalance direct climate change impacts on the ecosystem.

The effects of climate change on other river ecosystems should be modeled in order to investigate other ecosystem responses and regulation mechanisms. The response of one ecosystem gives an incomplete picture and it should be kept in mind that modeling always includes a certain level of uncertainty and that climate projections cannot provide precise forecasts. In the scope of a modeling study on the Elbe, stronger effects of climate change on phytoplankton biomass with changes of more than 100 µg L^{-1} were found (Quiel et al. 2011). In the Elbe, with a lower specific run-off compared to the Rhine, different regulation mechanisms prevail, for instance, effects of the changes in discharge might be more pronounced and losses to benthic filter feeding mussels are negligible.

The results of the present thesis suggest that assessments of potential impacts of climate change on biological processes in river ecosystems require a basic knowledge about the most important climate-related regulation factors on the one hand and about ecosystem responses towards these factors on the other hand. Concerning the future state of the rivers Rhine and Elbe, climate-related reductions in discharge will probably have the most pronounced effect on phytoplankton dynamics. For the Rhine, this probably implies a shift in the occurrence of the spring bloom and net increases of phytoplankton biomass along the river during low flows might be superimposed by losses to benthic filter feeders up to a certain degree. In contrast to the weaker response of phytoplankton in the Rhine, the ecosystem of the Elbe might be more sensitive towards direct effects of climate change.

6 Summary

This study addresses the regulation of large river phytoplankton by climate-related drivers with the help of three different approaches, i.e. analyses of long-term data and spatial dynamics (longitudinal samplings) as well as mathematical modeling. The central hypothesis is that discharge has a dominant role among climate-related variables which strongly alters phytoplankton biomass development. A multi-factorial statistical analysis on the basis of long-term data (1990 – 2009; 1994 – 2009) from two measuring stations of the rivers Rhine and Elbe revealed that discharge conditions and light availability were the main driving forces regulating phytoplankton spring bloom dynamics. For the Rhine, a trend towards an earlier occurrence of the spring bloom event and a decrease in seasonal mean phytoplankton biomass could be detected, whereas for the Elbe no shift in the timing of the spring bloom and a tendency towards increasing seasonal mean phytoplankton biomass was found. Longitudinal sampling campaigns served to analyze the spatial plankton development on a short-term scale. River-internal growth and loss processes, as well as import mediated by tributaries were examined. Four longitudinal profiles were realized at different seasons in recent years (2009 – 2011) and it was revealed that tributaries mainly had a diluting impact on plankton densities in the Elbe and provided an additional import of phyto- and zooplankton densities in the Rhine. In the present study, high bivalve abundances were detected in the Rhine, probably leading to river-internal losses of phytoplankton which could compensate phytoplankton production resulting in low phytoplankton concentrations. In the Elbe, low abundances of bivalves and a low benthic grazing pressure prevailed. On the other hand, an unusually low discharge event in spring 2011 in the Rhine demonstrated that loss processes can at times be superimposed by strong phytoplankton production leading to extremely high phytoplankton biomasses and chlorophyll *a* values. Hence, despite the observed long-term trend of decreasing chlorophyll values in the last two decades, extreme environmental conditions can provoke regime shifts with exceptional phytoplankton mass developments. To assess the potential impacts of future climate change on water quality, the water quality simulation model QSim was used to establish a model for the free-flowing part of the Rhine. The modeling approach was implemented by changing the hydrological and climatologic input data according to different climate projections for the near (2021 – 2050) and the far future (2071 – 2100). The model results indicated a weak response of phytoplankton biomass in the Rhine towards altered climatic conditions, including discharge reductions and water

temperature increases. The study suggests that changes in discharge rather than water temperature mediate climate change effects on large river phytoplankton. However, the effects are river specific as a consequence of system specific differences in main control mechanisms (e.g. ‘bottom-up’ versus ‘top-down’).

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8 Abbreviations

BfG	Federal Institute of Hydrology
DWD	German Weather Service
GCM	global climate model
Hydrax	hydrodynamic model
ICPR	International Commission for the Protection of the Rhine
MQ	mean discharge
NM7Q	lowest arithmetic mean discharge values during 7 successive days
NSE	Nash-Sutcliffe-Efficiency
orthoP	ortho-phosphate
PAR	photosynthetically active radiation
QSim	water quality simulation model
RBC Elbe	River Basin Community Elbe
RCM	regional climate model
TOC	total organic carbon
TP	total phosphorus
WSV	Federal Waterways and Shipping Administration

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Erklärung

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